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MFS - Stock Assessment

MANUAL OF METHODS FOR FISH STOCK ASSESSMENT

Part I. FISH POPULATION ANALYSIS

by
J. A. Gulland

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, 1965

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MANUAL OF METHODS FOR FISH STOCK ASSESSMENT

PART I. FISH POPULATION ANALYSIS

by

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(Containing revisions to Chapters 4.4, 4.5, 6, 9.3 and 11)

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MANUAL OF METHODS FOR FISH STOCK ASSESSMENT

PART I. FISH POPULATION ANALYSIS

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Section I. ESTIMATION OF PARAMETERS

1. MATHEMATICS AND STATISTICS

1.1 Mathematics

Fish population studies are essentially quantitative in character and therefore must involve mathematics to a large extent. In particular the quantitative aspect using relatively simple mathematical techniques is used throughout the subject. More advanced mathematics are used but are not usually essential, in the sense that much the same result can often be obtained without them, though at the cost of considerable extra labour. Most mathematical methods are here introduced and developed in connection with their particular application. However, powers, logarithms and exponentials are used so widely in the subject that they are best dealt with at once. They are essentially the same concept; for instance the logarithm of a number to the base 10 is that power of 10 which is equal to the number, e.g. $\log 10 = 1$, $10^1 = 10$; $\log 100 = 2$, $10^2 = 100$. This result for whole numbers can be extended to any number, e.g. $\log 2 = 0.30$, $10^{0.30} = 2$.

Logarithms need not be taken to base 10; any number will do, e.g. to the base 4, $\log_4 2 = \frac{1}{2}$; $\log_4 32 = 2.5$; $4^{2.5} = 32$. In particular natural logarithms are taken to the base e, where e (the exponential) is approximately equal to 2.72; these logarithms have very considerable advantages. Some work can be appreciably shortened by the use of special logarithmic graph paper. In this equal distances along the axis represent equal logarithmic increments; thus plotting x on log paper has the same result as plotting log x on ordinary graph paper.

The chief use of exponentials lies in their application to the study of mortalities. If a stock of fish is subject to a certain steady cause of mortality, then the rate (i.e. numbers per unit time) at which fish are dying will be proportional to the mortality and to the number of fish present. That is, if N is the number of fish, and Z the (instantaneous) mortality coefficient

$$\frac{dN}{dt} = -ZN \qquad (1.1)$$

If the number of fish originally present at time t = o is N_o, then the equation has the solution, giving the numbers at time t

$$N_t = N_o e^{-Zt}.$$

This form for mortalities enables the number alive at any time (and hence the number dying in the previous period) to be calculated directly. The combination of two independent causes of mortality is also simple, for from the form of equation (1.1), if Z' is some other cause of mortality, the rate at which fish are dying due to it is

$$\frac{dN}{dt} = -Z' N,$$

and hence the total deaths are given by $\frac{dN}{dt} = -(Z + Z') N$

and hence $N_t = N_o e^{-(Z + Z')t}$

i.e. the mortalities are simply additive. The advantages of this method of describing mortalities will be seen at once when dealing with the examples.

1.2 Statistics

Fish population studies involve the measurement and analysis of many quantities - e.g. age-compositions, and growth rates - few of which can be measured exactly, either because of their inherent variability or the difficulty of measurement. Statistics must therefore be used to some extent, if only in such a simple form as taking the mean of a set of values. Basic statistical methods are the same whatever the subject in which they are being applied, and are described in many text books. These notes will therefore only deal very briefly with the basic methods. Some applications, e.g. correlation and regression analysis will be dealt with later as they occur. In this section most attention will be paid to the problem of sampling fish populations. (Statistics is dealt with in more detail in another manual in this series, in which both the basic methods and special applications to fisheries are described).

In statistics we are concerned not so much with any individual value, e.g. the size of any one particular fish on the fish market, but with the frequency with which the various values (e.g. sizes of fish) occur. Such frequency distributions may be represented graphically, either as histograms or frequency polygons. Much of the frequency distributions can be described by two quantities; the

average value (or the position of the curve) and the spread. The most common measures for the average are the arithmetic mean (or simply mean), the median (or half way value) and the mode (or most frequent). Of these the mean has most advantages. The common measure of dispersion is the variance, which is the average of the square of the deviation from the mean; the square root of the variance is the standard deviation. Further discussions of these measures, together with methods of calculation etc may be found in most text books, e.g. Yule and Kendall, Chapters 4, 5 and 6.

Tests of significance are another group of statistical tools of great use in fishery research, as in most other fields. While the explanation of the arithmetical steps involved in any particular test will be left to the appropriate section of the text books, e.g. Yule and Kendall, Chapter 21, it is worth emphasizing here the underlying basis of tests of significance. That is, we assume some nul hypothesis, and on this basis calculate the probability of the observed values occurring. If this probability is sufficiently small (usually one in twenty, or one in a hundred) we reject the nul hypothesis. For instance, using the t-test for the difference in the means of two samples, the nul hypothesis is that the two samples come from the same population. If the probability of a value of t equal to or greater than that observed occurring is say 0.01, this means that if the two samples had come from the same population, an unlikely even (a one in a hundred chance) has taken place and we therefore believe that the two samples did not come from the same population, i.e. they are statistically different. Such a test does not give any information on the probability of the two samples coming from different populations, or on the practical significance of the difference. For instance, two small and variable samples may differ by an amount which is not statistically significant, but which if real would be most important. Conversely, for two large and homogeneous samples a difference may be large enough to be statistically significant, but yet so small as to be negligible in practice.

1.3 Sampling (For further details see Part I of Manual of Sampling and Statistical Methods for Fisheries Biology)

Most of the quantities involved in fish population work cannot be obtained or measured throughout the whole population; e.g. it is virtually impossible to measure all fish caught, even less all the fish in the sea. A section, or sample, of the whole population is therefore examined for the attributes concerned, e.g. percentage of mature fish, or average size. On the assumption that this sample is representative of the whole population, an estimate may be made of the true value in the population. If the sampling system used is a good one, then the estimate obtained will differ little from the true value. The merits or otherwise of a sampling system can therefore be measured by two quantities relating to the estimates obtained (those measures refer not to any individual estimate, but to the set of estimates which might be obtained by repeated samples); firstly, the variance, which as defined above for any statistical distribution, is the measure of the scatter of the estimates about their mean value; secondly, the bias, which is the extent to which this mean value differs from the true value. (The term bias is also used for the processes leading to this difference).

Because when a bias exists, it exists in all samples, tending to make the estimates constantly greater (or less) than the true value, it cannot be detected as a difference between repeated samples; thus in general bias is very difficult to detect, and hence eliminate, in subsequent analysis. A large variance, in contrast, appears at once in the differences between samples. Large bias is therefore even less desirable than large variance, in that it may cause what appear to be reliable and consistent data to give results that are consistent only in the extent to which they are wrong.

The basic feature of any good sampling system is a "random" sample. The aim of a random sample should be to ensure that all members of the collection of objects being sampled have the same chance of occurring in the sample. In practice this condition may be relaxed and the sampling be non-random so long as there is no relation between the chance of occurring in the sample, and the value of the attribute being measured. For instance, the first fish unloaded from a trawler onto the fish market is usually one of the last caught and will be placed near the edge of the array of fish and therefore have a better chance of appearing in the sample. If we are only concerned with sampling for the size of fish, this may not matter as there is little relation between size of fish and time of capture, but the sample would be a very bad one if we were concerned with the condition or freshness of the fish. The main damage done by non-random sampling is this introduction of bias (e.g. that the sample taken above will be biased towards having too many fresh fish) though non-random sampling has other disadvantages, e.g. that many of the calculations used for estimating variance etc are only valid for r ndom samples. The first concern in taking a sample is therefore to ensure that no form of selection can occur that might cause a bias. Such selection may be very obvious and direct, e.g. the tendency to take the bigger fish from a pile, leaving the smaller until last, but may be much less obvious; e.g. in the East Anglian herring season it would seem convenient to take samples of herring from the first drifters arriving each morning. These tend to be from the nearer grounds, which in turn tend to have slightly different size and age of fish. Thus a non-randomness in time of sampling causes a bias in the estimate of average size or age of fish landed.

The practical difficulties in taking a truly random sample from a large and heterogeneous collection of objects are considerable. These difficulties may be overcome by dividing up the whole collection

into smaller and more compact sections, within which a random sample may be taken fairly readily. Two such methods of sampling are stratified and two-stage sampling. In stratified sampling the whole collection of objects is divided into several sections, or strata, each of which is then sampled and analysed separately, e.g. landings at different ports may be taken as strata. This method is particularly useful in reducing bias and variance when there is a marked difference between strata.

The chief sampling problem in fish population studies occurs when obtaining indices of abundance of the different ages and sizes of fish, and particularly in sampling the commercial catches for size and age composition. Before starting to consider the sampling procedure, the objective of the sampling must be defined, both in extent and the attribute being examined, e.g. length of plaice landed by English trawlers from the North Sea. Following a stratified sampling scheme the complete population, which will be rather heterogeneous, may then be divided into fairly uniform strata. For English demersal landings it was found suitable to treat landings at each port and in each month separately, but for the more variable herring landings, landings in three-day periods were chosen. The first step in the actual sampling procedure is to ensure that the sample taken is not biased. Once the catch of a vessel is sold it may be divided amongst a number of merchants each of whom is almost certain to prefer a certain size or quality of fish; therefore any sample from the purchases of one merchant is almost certain to be biased. Sampling of commercial catches must therefore be taken before the catch is divided; in England this means sampling in the early morning while the catch is laid out on the fish market before being auctioned.

The choice of fish to measure is conveniently done in two stages; first a sample of one or more ships from the whole fleet landing during the period, and then measuring a sample of fish from the chosen ship or ships. The choice of ships to sample is usually straightforward and minor departures from non-random samples are not very likely to be harmful, but may introduce bias when time of landing or position on the market (which are likely to influence their chance of being sampled) are themselves influenced by the fishing ground, and hence related to the composition of the catch. This difficulty may be overcome by further stratification, sampling and analysing the catches from each area separately.

When taking a sample of fish from a ship's catch an important source of bias is the tendency of most people to take first the largest fish from a pile and to leave the smallest to last. This is especially noticeable when sampling fish on deck, e.g. a haul of a research vessel. At sea this bias can only be overcome by handling all the catch, or at least a predetermined part (e.g. one corner), clearing all the fish right down to deck level. On the market most fish are laid out in boxes (often with the larger fish of the box on top), and bias will be avoided by sampling one or more complete boxes. If there is no definite sorting into two or more categories, systematic differences between boxes are unlikely and a convenient but non-random method of sampling, e.g. taking boxes from one edge of the landing, is justifiable. Important in working up the results of such a sampling system are the raising factors, i.e. ratios of weight sampled to total weight landed, both over the whole landings and within a sampled ship. The procedure is as follows; supposing we are interested in the total number landed of a certain size (or age, maturity, etc) of fish

Let m = number of ships from which samples were taken and for any particular one of these, say the ith,

W_i = weight landed
w_i = weight sampled
n_i = number of fish of required size in sample

then $W_i/w_i = r_i$ = raising factor for i^{th} ship

and hence $n_i r_i = n_i W_i/w_i$ = number of fish of required size in sampled ship.

Adding up for all sampled ships gives the number of fish of required size for all sampled ships, as

$$\sum_1^m n_i r_i = n \text{ say.}$$

Also if W = total weight landed
and w = weight landed by sampled ships
then R = raising factor = W/w
and $Rn = n\,W/w$ = total number of fish of required size landed
= N say.

That is $N = W/w \sum n_i W_i/w_i$

Frequently fish are sorted into several size categories which may or nay not be the same from one ship to the next; then obviously a sample must be taken from each category of the ship examined. The figure for the ship as a whole is then given by raising each category individually by the appropriate raising

factor. Thus, supposing there are two categories, using the notation above, and using one or two dashes to distinguish the different categories, we have

$$r'_i = W'_i/w'_i;\ r''_i = W''_i/w''_i$$

and number of fish of given size on the ith sampled ship is

$$n'_i\, r'_i + n''_i r''_i = n'_i\ W'_i/w'_i + n''_i\ W''_i/w''_i$$

Then the total number landed may be estimated directly as

$$N = R\sum\left\{n'_i\, r'_i + n''_i\, r''_i\right\}$$

Alternatively, and rather better, the sorting by categories can be used as stratification through all landings, and raising factors for each category calculated and applied. Then the estimate of the numbers landed is

$$N = R'\sum n'_i\, r'_i + R''\sum n''_i\, r''_i$$

where $R' = W'/w';\ R'' = W''/w''$

This second estimate will be more precise (have less variance), as it utilizes the information on the division of all landings between the categories. It can be applied so long as the sorting is constant even if not very accurate, i.e. the number and definition of the categories is constant, even if the dividing line between them is variable.

In population studies we are interested in several characteristics of the fish, e.g. length, weight, age, maturity, most of which are closely related. Some, e.g. lengths, are very easy to determine both quickly and accurately even under the somewhat adverse conditions at sea or on the fish market. Other characteristics, e.g. age, which are considerably more tedious to determine are then most easily determined by sampling directly for length only, and using relatively small age samples to establish an age-length key for converting length composition to age composition. That is, the length sampling gives the number of fish in each length-group, and the age samples give the proportion of each age within each length-group. The number at each age is then readily given; algebraically if

N_i = number of fish in i^{th} length-group
P_{ij} = proportion of fish of age j in i^{th} length-group

where $P_{ij} = n_{ij}/n_i$

n_i = number of length i examined for age
n_{ij} = number of length i examined which were age j
then $N_i P_{ij}$ = total number of fish of length i and age j

and $\sum N_i P_{ij}$ = total number of fish of age j.

It should be noted that these calculations involve no assumptions concerning the pattern of growth, though the advantages of the method in form of increased accuracy (decreased variance and risk of bias) are greatest when the growth is fast and uniform.

Sampling the Population

Data on the composition of the catch are important in themselves, particularly when comparing and combining the effects of two dissimilar fisheries exploiting the same stock; or in making assessments of the immediate effects of, say, a mesh change. The catch, whether of the commercial fleet or of a research vessel, may also be considered as a sample of the stock. The usual sampling methods are directly applicable, e.g. stratified sampling by dividing the region into fairly uniform sub-areas, but special problems arise in obtaining unbiassed estimates of the abundance and the composition of the stock. The first is a matter of relating stock density to catch per unit effort, and the second of selection in the widest sense, i.e. including any factor making one size (or condition) of fish more likely than another to be caught and retained by the gear, with mesh selection included as a special case. These latter problems will be discussed more fully in the appropriate later sections.

1.4 Exercises

1.41 Mathematics. Use of powers, logarithms and exponentials.
Give the values of 10^0, 10^2, 2^6, 4^0 $4^{\frac{1}{2}}$, $9^{1.5}$, $8^{2/3}$, 7^{-1}, 3^{-2}, $4^{-0.5}$, $4^{-1.5}$
Using the appropriate tables, give the values of

(i) $\log_{10}$ of 2, 360, 0.40, 0.07
(ii) $\log_e$ of 2, 2.72, 10, 20, 360, 0.40, 0.99, 1.016, 1.007,
What is the ratio of $\log_{10}$ to $\log_e$ for the above numbers?
(iii) $10^{0.30}$, $10^{2.56}$, $10^{-0.60}$, $10^{-1.70}$,
(iv) $e^{0.70}$, $e^{2.30}$, $e^{3.00}$, $e^{5.86}$, $e^{-0.90}$, $e^{-0.01}$, $e^{0.016}$, $e^{0.007}$, $e^{-0.007}$.

From looking at the results of the last four examples, can you give, without using tables, approximate values of $e^{0.006}$, $e^{-0.010}$.

(v) Give the values of x in the following equations
$e^x = 10^3$, $\exp(x) = 10^{-0.1}$, $10^x = 4^3$, $e^{-x} = \log_{10} 7.3$

(vi) A population is subject to a mortality giving an instantaneous mortality coefficient of 0.5; give, as a percentage of the initial numbers, the numbers after 1 year, 2 years, 6 months. Repeat for mortality coefficients of 0.1, 1.2, 0.7.

(vii) A certain mortality causes 25% of the population to die each year; what percentage of the initial population is left after 2 years; 6 months; 3 years. What is the corresponding instantaneous mortality coefficient. (N.B. find the coefficient first). Repeat for mortalities causing 10%, 90%, 50% mortalities per year.

(viii) Two causes of mortality, acting independently, cause mortality coefficients of 0.2 and 0.3; what is the resulting total mortality coefficient?
Repeat with coefficients of 0.7 and 0.1; 1.0 and 0.3.

(ix) Two causes of mortality act independently on a population; alone they would cause respectively 20% and 30% of the population to die within a year.
Do 50% of the population die within a year?; if not, what is the percentage that does die (N.B. convert to instantaneous mortality coefficients).
Repeat for pairs of mortalities causing 70% and 30%; 80% and 70% mortalities.

(x) Plot y against x, on semi-logarithmic paper, and $\log_{10} y$ and $\log_e y$ against x on ordinary graph paper.

x	0	1	2	3	4	5	6
y	1.12	1.58	2.24	3.16	4.47	6.31	8.91

Do the points satisfy the equation

$$\log y = ax + b$$
$$\text{or} \quad y = c\,e^{dx} \quad ?$$

If so, what are the values of a, b, c, d?

(xi) Repeat (x) for the two sets of y

x	0	1	2	3	4	5	6
y_1	0.79	0.63	0.50	0.40	0.32	0.25	0.20
y_2	0.71	0.35	0.18	0.089	0.045	0.022	0.011

If the y's are indices of the density of a certain year class of fish at yearly intervals, do the data fit a constant mortality coefficient?; if so, what is the fraction surviving each year, and what is the instantaneous mortality coefficient.

1.42 Statistics and Sampling.

1. Given the two length frequency distributions

Length (cm)	10	11	12	13	14	15	16	17	18	19	20
Frequency	1	3	8	16	18	17	12	6	2	1	0

and

Length (cm)	10	11	12	13	14	15	16	17	18	19	20	21	22
Frequency	0	0	4	12	14	10	9	8	4	3	1	1	0

determine the following:-

(a) Mean
(b) Mode
(c) Median
(d) Variance
(e) Standard deviation
(f) Standard error of each mean.

Using these results, determine whether the difference between the means exceeds twice (the 5% level) or three times (the 1% level) its standard deviation. (note that the mode is most readily determined graphically; the others by calculation).

2. Repeat (1) for the two distributions

(a) 15, 17, 20, 23, 24, 27, 29, 31, 33, 35, 36, 36, 38, 40, 42, 42, 46, 49, 52, 53, 54, 58, 60, 65, 71

(b) 19, 26, 23, 29, 30, 32, 34, 37, 38, 40, 42, 42, 44, 45, 46, 48, 51, 54, 56, 59, 60, 65, 68, 75

3. One ten stone box of each, of large, medium and small hake were sampled on each of two trawlers. The numbers recorded, in each 10 cm group, and the weights landed were

Length group		40-	50-	60-	70-	80-	90-	100-	Total	Weight landed (boxes)
Ship A	Large					7	7		14	2
	Medium			8	15	3			26	10
	Small	2	32	19	1				54	14
Ship B	Large					5	4	3	12	23
	Medium			4	17	6	1		28	53
	Small	1	13	27	4				45	40

The numbers of boxes landed by all ships were Large 350, Medium 720, Small 1,056. Calculate the number of 60-69 cm and 80-89 cm hake landed by the sampled ships, and the total by all ships.

4. The estimated number of male plaice landed in 1955 at Lowestoft in each 5 cm group were:-

25-29	30-34	35-39	40-44	45-49
3,991,984	4,155,009	1,232,174	274,972	15,346

The number of male fish whose otoliths were taken, and their estimated ages, were:

Age	3	4	5	6	7	8	9	10	11+	Total
Length										
25-29	33	82	30	13	8	1				167
30-34	8	48	53	24	34	12	5	1	1	186
35-39	1	14	26	33	42	19	11	10	6	162
40-44		1	8	2	12	5	5	-	3	36
45-49						1	4	-	4	9

Estimate the total number of six year old fish landed.

5. Discuss sampling problems and methods as they occur in fisheries with which you are familiar.

2. GROWTH

The basic requirement is an expression which will give the size (in terms of length or weight) at any given age which agrees with the observed data of size at age, and which is in a mathematical form which can be incorporated reasonably easily in expressions for yield. Strictly, most population analysis is concerned more directly with growth rate, i.e. increase in weight or length per unit time, rather than with the size at various ages, because many problems in fishery assessment are essentially a matter of comparing weight gained by growth against that lost by natural mortality. Sometimes, for instance when considering the effect of an increase in size of first capture, it is particularly important to know the rate of growth over a comparatively short part of the total life-span - that is, to know how long it will take a fish to grow from the original size of first capture to the new. There are therefore good reasons for preferring, other things being equal, a method of fitting equations to growth rate data, rather than simply size at age.

Other desirable features of a growth equation are that the computational work involved in fitting it to observed data should be small, that the number of constants used should be few, that as far as possible these constants should have some biological meaning, and that if extrapolated to ages beyond those used in fitting the equation, the equation should not lead to unreasonable results.

There exists a considerable and growing literature on growth equations, which covers a wide range of possible equations, none of which seems to be entirely satisfactory in all situations. In fact it is most unlikely that a simple formula would always be able to describe the growth of even a single fish through most of its life, in which there could be greatly different conditions of food supply, reproductive strain, etc. These notes do not attempt to give a complete survey of growth equations, but will be mainly concerned with one particular equation, that ascribed to von Bertalanffy, which satisfies the two most important criteria - it fits most of the observed data of fish growth, and can be incorporated readily into stock assessment models.

If the length of a fish, crustacean, or lamellibranch is plotted against age, the result is usually a curve of which the slope continuously decreases with increasing age, and which approaches an upper asymptote parallel to the X-axis. Curves of weight at age also approach an upper asymptote, but usually form an asymmetrical sigmoid, the inflexion occurring at a weight of about one-third of the asymptotic weight.

If the rate of growth in length, i.e. $^{dl}/dt$, is plotted against length, the result is often well fitted by a straight line, cutting the X-axis at a point L_∞ beyond which the fish will not grow. This is of course the asymptote of the plot of length on age. If the increase in length is linearly related to length, then in mathematical terms

$$\frac{dl}{dt} = K\,(L_\infty - l) \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (2.1)$$

so that $l - L_\infty = c\,e^{-Kt}$, where c is a constant.

Re-writing, and changing constants

$$l_t = L_\infty\,(1 - e^{-K(t-t_o)}) \quad \ldots\ldots\ldots\ldots \quad (2.2)$$

where $c = -L_\infty\,e^{Kt_o}$

Equation (2.1) is identical with that deduced by von Bertalanffy on physiological grounds. He considered that growth in weight was the resultant of the difference between anabolic and katabolic factors, taken as proportional to surface area and weight respectively.

i.e. $^{dw}/dt = hs - kw$

or, putting $w \propto l^3$, $s \propto l^2$

$$\frac{dl}{dt} = H - Kl$$

In fitting the growth curve the instantaneous rate of growth will not be known, but only lengths at certain times - often one year apart when they are derived from age-determinations, but at irregular intervals if derived from tagging data. If the times t_1, t_2 are close together, a close approximation to the instantaneous rate of growth is given by $^{l_2-l_1}/_{t_2-t_1}$ where l_1, l_2 are the lengths at times t_1, t_2 respectively. If this growth rate is plotted against the mean length $(\frac{1}{2}(l_1 + l_2))$, then a plot corresponding to equation (1) is obtained; the intercept on the X-axis gives an estimate of L_∞, and the slope an estimate of -K.

For data at equal time intervals of length T, from equation (2.)

$$l_t = L_\infty (1-e^{-K(t-t_o)})$$

$$l_{t+T} = L_\infty (1-e^{-K(t+T-t_o)})$$

$$l_{t+T}-l_t = L_\infty e^{-K(t-t_o)} (1-e^{-KT})$$

$$l_{t+T}-l_t = (L_\infty - l_t)(1-e^{-KT}) \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (2.3)$$

The plot of increment, $l_{t+T}-l_t$, against initial length, l_t, therefore gives a line, slope $e^{-KT}-1$, and an intercept, on the X-axis, of L_∞. The important special curve is T = 1 year, when the slope = $e^{-K}-1$. An alternative form of equation (2.3) is

$$l_{t+T} = L_\infty (1-e^{-KT}) + l_t e^{-KT} \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (2.4)$$

which, for T = 1, is the well known Ford-Walford plot, of l_{t+1} against l_t, which gives a straight line, slope e^{-K}, and an intercept on the 45° line, where $l_t = l_{t+1}$, of L_∞. This plot is essentially the same as the plot of increment $(l_{t+1}-l_t)$ against initial length. The points will seem to fit the Ford-Walford line better, but because the intersection of the regression line and the 45° line is very oblique, L_∞ is in fact estimated with equal precision by the two plots, and if the fitting is done graphically rather than by calculating regression lines, e.g. by least squares, greater errors in drawing are likely to be introduced in the plot of l_{t+1} against l_t.

L_∞ and K can be determined directly from the lines fitted to these plots either by regression analysis, or by eye; then t_o can be estimated from equation (2.2) for any particular observation of length at age. For this, equation (2.2) is best re-written as

$$e^{-K(t-t_o)} = \frac{L_\infty - l_t}{L_\infty}$$

$$\text{or} \quad t_o = t + \frac{1}{K} \log_e \left(\frac{L_\infty - l_t}{L_\infty}\right) \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots (2.4)$$

While an estimate of t_o can be thus obtained for each age for which the mean length is known, these estimates will not be equally good. Those from old fish will be highly variable, because a small difference in l_t makes a big difference to the estimate of t_o when l_t is nearly equal to L_∞, while the mean length of the youngest fish may be biased because only the bigger fish of these ages appear in the catches. The best estimate of t_o would appear to be the mean of the estimates of t_o obtained from the younger, but fully recruited, age groups.

Alternatively, only L_∞ is estimated from the plots of increment against initial length. From this $\log_e \left(\frac{L_\infty - l_t}{L_\infty}\right)$ can be calculated, and plotted against t. From equation (2.4) this should give a straight line, slope $-1/K$, intercept t_o.

Data on length at annual intervals can be obtained and tabulated in various ways. Probably the most straightforward is the analysis of the growth of a single fish - the length at the end of each year of life being obtained from measurements along an axis of a scale, otolith or other hard structure. Alternatively, the growth of a single year-class can be followed over a period of years - i.e. for the 1956 year-class the increment in the fifth year of life is the difference between the mean length of five year old fish at the end of 1961 and four year old fish at the end of 1960. Both these methods are concerned with the growth of a group of fish during their life, the growth during each year of life providing one point in the plot. Thus the growth increments refer to different calendar years; for example for the 1956 year-class the increment in the third year of life is put on in 1959, possibly under conditions very different to those in 1961, the fifth year of life. Growth in a particular year can be studied by taking the growth of different year-classes - e.g. data of growth in 1960 are given by the growth of the 1956 year-class in its fifth year of life, of the 1957 year-class in its fourth year of life - each year-class provides one point in the plot. This is a particularly useful method for studying the effect of the environment - food, temperature, density, etc on growth. Finally, growth can be estimated from a single year's data, e.g. from data in 1960 the increment in the fifth year of life can be estimated from the difference in lengths of the 1955 and 1956 year-classes, the fourth year's increment from the difference between the 1956 and 1957 year-classes, etc. These

differences do not, in fact, correspond to the growth of any particular fish or group of fish, and the method should be used only when other methods cannot. An improvement is to take the average size at each age over a number of years, but in this case it is usually possible, and more satisfactory, to analyse the growth of the individual year classes or in each calendar year.

The weight of a fish is usually closely proportional to the cube of its length, so that from equation (2.2)

$$W_t = W_\infty \left(1-e^{-K(t-t_o)}\right)^3 \qquad \ldots\ldots\ldots\ldots\ldots\ldots \quad (2.5)$$

where W_∞ is the asymptotic weight, corresponding to the asymptotic length L_∞.

When growth data are given in terms of weight, fitting of growth curves is most easily done by using the cube-root of the weight as an index of length, fitting this to the equations of growth in length as above, and finally cubing to return to weight.

A more general growth equation has been given by Richards; with a slight change from his notation this is

$$w_t^{1-m} = W_\infty^{1-m} - ae^{-kt} \qquad \ldots\ldots\ldots\ldots\ldots\ldots \quad (2.6)$$

For various values of m this equation becomes one or other of the common growth equations. Thus if $m = 2/3$, equation (2.6) becomes the same as equation (2.2) for the von Bertalanffy curve. If $m = 2$ the equation, with some re-arrangement, becomes the autocatalytic equation

$$W_t = \frac{W_\infty}{1 + be^{-kt}}$$

and for $m = o$, the monomolecular equation

$$w_t = W_\infty \left(1-be^{-kt}\right)$$

2.1 Exercises

1. The von Bertalanffy growth equation contains three parameters (L_∞, K and t_o), which can therefore be estimated from three observations of length at age. From equation (2.2) write down the lengths at times t-1, t, t+1, and the increments in length between t-1 and t and between t and t+1. Hence determine an estimate for K from the ratio of these increments; by substituting this estimate for K in equation (2.2), or otherwise, find an estimate for L_∞, in terms of l_t and the increments.

2. Kitahama and Hitoshi (1955) give the following size-at-age data for the Pacific herring, Clupea pallasii C. and V., caught off the western coast of Hokkaido from 1910-54. The lengths are averages over a forty-five year period; ages determined from scale rings.

Age (yrs)	Total length (cm)
3	25.70
4	28.40
5	30.15
6	31.65
7	32.85
8	33.65
9	34.44
10	34.97
11	35.56
12	36.03
13	35.93
14	37.04
15	37.70

$W = 7.8 \times 10^{-3} L^3$ gm

(a) Construct a work-sheet and determine L_∞, W_∞, K and t_o.

(b) Calculate the theoretical curves of growth in length and weight over the range 0-15 years.

3. Yokota gives the following data for growth of the shark Mustelus kanekonis (age determined from seasonal changes in length of claspers).

Age Groups	Weight (gm)
I	375
II	1,519
III	2,430
IV	3,247

$$W = 7.4 \times 10^{-3} L^{3} \text{ gm}$$

(a) Determine L_∞, W_∞, K and a working value for t_o.

(b) Calculate curves of growth in length and weight up to age-group VIII.

4. Posgay (1953) tagged sea-scallops, and obtained the following data on growth during the ten months (approximately) between tagging and recapture.

Shell Diameter (mm)

At tagging	64	69	71	94	104	105	110	117	117	126
At recapture	98	102	93	115	120	126	125	127	136	138

(a) Calculate L_∞ and K.

(b) Taking $t_o = 0$, calculate and plot the curve of growth in length up to six years.

5. Ochiai (1956) gives the following data for the growth of the soles Heteromycteris japonicus and Pardachirus pavoninus.

Age (yrs)	Standard length (cm)	
	H. japonicus	P. pavoninus
1	6.09	10.00
2	8.10	14.80
3	9.20	

(a) Determine arithmetically L_∞, K and t_o for each species (assume $t_o = 0$ for P. pavoninus).

(b) Demonstrate the patterns of growth in weight, assuming a cubic relation of weight to length.

6. Moiseev (1946) gives the following data for growth in total length of the flatfish Limanda aspera in Peter the Great Bay (Japan Sea).

Age	Sex	Sampling Year				
		1928	1930	1931	1932	1933
1	♂	5.15	7.60	6.58	7.72	8.34
	♀	5.77	7.22	7.20	9.50	7.34
2	♂	10.25	13.60	11.70	13.80	14.10
	♀	11.77	11.88	13.20	15.50	12.68
3	♂	16.40	19.40	17.42	18.82	19.44
	♀	17.41	19.00	18.80	21.00	18.68
4	♂	20.45	24.00	21.22	22.92	24.32
	♀	22.13	25.00	23.60	25.50	25.32
5	♂	25.05	26.80	25.42	26.38	27.66
	♀	26.51	26.12	27.60	29.50	27.32
Index of total demersal catch		1	1	5.5	8.0	7.7

(a) Analyse sexual differences in growth.

(b) Bearing in mind that large-scale fishing was started in the Bay only in the season 1929-30, and that L. aspera formed 80% of the demersal catch, examine the year-to-year variation in growth.

(c) The mean age composition by number, during 1931-33, was as follows:-

Age	3	4	5	6	7	8	9	10	11	12
%	0.6	4.7	16.1	33.3	27.9	11.3	3.4	1.7	0.9	0.2

Estimate the total mortality coefficient and examine the growth data for bias in mean length at age, due to selection.

3. EFFORT AND CATCH PER UNIT EFFORT

These two quantities may be conveniently treated together. Both provide indices proportional to important quantities - the instantaneous fishing mortality coefficient and the density of the exploited stock. Also if the total catch is known (as it generally is), then if either of the quantities is known the other can be calculated at once. Though catch per unit effort is usually a derived quantity obtained from the independent values of catch and effort, these data need not relate to an entire fishery, and in practice the catch per unit is often obtained from data from some part of a whole fishery, and the total effort is estimated from it.

Though the catch per unit effort will rarely be exactly proportional to the stock density, it is often essential to have some measure of the stock, and the catch per unit will nearly always be the best available - better than, for example, total catch. As knowledge of the fishery increases, requiring better indices of stock magnitude, so, in general will the measure of catch per effort become better, being refined by taking into account the spatial distribution of fishing, differences in the fishing power of vessels, etc.

The relations between catch, effort and stock density are clear for the operations of a single unit on a uniform density of fish, e.g. a trawl which may be considered as taking at each haul a fixed proportion of the fish present. Then the catch per operation is proportional to the stock density, and the number of operations is proportional to the mortality caused.

These relations may be easily extended to cover the activities of the whole fishery, provided that the efforts of the whole fleet are expressed in the same units. The fishing effort of a single unit is for most types of gear best defined as the product of its fishing power and the number or duration of its operations. The first problem is therefore to define the unit operation; this may be simple, e.g. an hour haul for a trawl, but for other gears, especially those for which an important part of the time is spent searching for the fish, the appropriate unit of fishing time may not be at all obvious. The fishing power of a particular fishing unit can be defined relative to some standard fishing unit or units of gear, as measured by their respective catches per unit or operation when fishing at the same time and place (or at least on the same density of fish). As the fishing effort is itself only a proportional index of the important quantity - the fishing mortality coefficient - it is legitimate to use any quantity proportional to fishing effort or fishing power as an index of effort or power. For instance it has been shown that for English trawlers the fishing power is proportional to gross tonnage; thus the quantity from tonnage x hours fishing gives a serviceable index of fishing effort for English trawlers.

Appropriate units of fishing time and fishing power may now be suggested for some types of gear.

Gear	Time	Fishing Power
Trawl	Hours fishing	Size of vessel; tonnage; horse-power
Danish seine	" "	? Apparently independent of vessel characteristics
Long-line	" "	Number of hooks
Drift net	" " Number of hauls	Number of nets; length or area of nets

With some other methods such as purse seining, ring netting and whaling the fishing operation includes a longer or shorter time looking for the shoals of fish, or whales, during which no actual fishing is done. For these methods the proper unit of fishing effort would appear to be a measure of the area searched. Fishing time would be measured by time spent steaming (excluding if appropriate the time between port and likely fishing grounds), and fishing power by such factors as speed and searching equipment (echo-sounders, Asdic, etc). Catch per unit effort could be expressed as catch per hour steaming, or per area searched, and if the searching was fully efficient, and all the fish or whales seen were caught, the catch per area searched would give an absolute measure of density, rather than only an index. The catch per unit effort of a shoaling fish may often be usefully considered in two parts - the number of shoals estimated from the numbers of sightings or hauls per unit searching time, and the size of shoals estimated from the catch per haul.

The list of units suggested here is not exhaustive, nor indeed are the units necessarily the best; the choice of unit of effort must depend on the particular circumstance of each fishery. For instance, if weather often interferes with the fishery, making fishing impossible for a considerable and variable part of some seasons, the number of boats would be an unsuitable measure of effort; the total number

of hauls made would give a better measure. To a certain extent, however, the defects of this sort of incorrect measure of effort, which departs from the true value because of (probably) random effects of weather, are much less important than those of wrong measures which depart systematically from the true value. One such departure occurs when there has been a steady increase in the fishing power of the gear in use. For instance, the average size of the English trawlers fishing at Iceland has about doubled over the past thirty years, and as a result the catch of cod per hour has also increased steadily, although the use of the better measure of catch per unit effort - catch per ton-hour - shows that the average density of cod has in fact not changed appreciably. Another very misleading type of effort unit is that for which the relation between the recorded effort and true effort is dependent on the density of stock. This dependence may be due to a loss of fishing power caused by gear saturation, e.g. the reduction of available hooks on a long-line, or by reduction of effective fishing time, e.g. in the English distant water trawler fleet the number of hours actually spent fishing per day at sea is reduced during times of heavy fishing by the need to spend extra time gutting and stowing the catch; for this fishery, days-at-sea is therefore not a proper unit of fishing time.

Normally the total effort of a fleet will be equal to the sum of the effort which would be expended by the individual ships if they had been fishing alone, but if the presence of many ships helps the fleet to concentrate on the fish by more efficient searching, the effective effort will be higher; conversely the presence of a large fleet may (e.g. by frightening and dispersing the shoals) interfere with the efficient working of the ships, and reduce the effective effort.

When more than one group of vessels is exploiting a unit stock - e.g. otter trawlers and long-liners, or vessels from several countries - it will usually be difficult or impossible to express the effort statistics from all vessels in the same units, and thus to obtain directly a figure for total effort. One single fleet (A) may therefore be taken as standard, and its catch per unit effort taken as the best index of density, and total effort estimated as

$$\text{Total effort} = \text{Effort of Fleet (A)} \times \frac{\text{Total catch}}{\text{Catch of fleet (A)}} = \frac{\text{Total catch}}{\text{Catch per unit effort of fleet (A)}}$$

If reasonable effort statistics are available from more than one fleet it is best first to calculate catch per unit effort figures for each fleet separately, and then compare the year-to-year changes in the indices of abundance thus obtained. If each separate index follows much the same trend, then this is some confirmation that each is a fair measure of the abundance (the degree of confirmation increases with the diversity of the fleets concerned - e.g. it is more encouraging if data from trawlers and long-liners agree, than if two trawl fleets agree). Conversely, if there is a discrepancy between two sets of catch per unit effort figures, then one, and possibly both, is not a good measure of abundance. Before using either set of data the methods of obtaining them must be examined to see where the discrepancy might arise (e.g. one fleet has included an increasing number of new and powerful vessels, not taken account of in the effort statistics used). If two or more fleets give consistent indices of catch per unit effort, then a single pooled index of catch per unit effort (and hence of total effort) can be conveniently obtained by expressing the index for each fleet as a percentage of some standard year, or period of years.

When the fishing power and fishing time have been fully standardized, the resulting catch per unit effort will be proportional to the average density at the positions fished, the average being weighted according to the amount of fishing at each place. This average density will almost certainly be greater than the true average density, because most fishing will be done on the grounds giving good catches. The catch per unit effort will, however, still be a valid index of the density so long as the ratio of the true density to the density weighted by the amount of fishing remains fixed. The difference between the true average density and the average density taken over the positions fished may be considered in two parts. On any given fishing ground, which for the North Sea trawl fisheries may be thought of as say ten miles across, the distribution of fishing will be determined solely by the fishermen's ability to find the small local concentrations of fish. The density in the unfished areas will be unknown, but the ratio of the density in the fished areas to the average density will generally be constant, at least over a short period. Over a longer period the introduction of new devices may permit the fishermen to concentrate more effectively on the fish, either directly (echo-sounding) or by more accurate navigation (e.g. Decca, radar or echo-sounding). To the first approximation, though, we may write

$$C/_f = q^1 \bar{D} = qD \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots (3.1)$$

where C = catch, f = effort

q, q^1 are constants

and $\bar{D}$ = density, weighted by amount of fishing
D = true average density.

A unit stock will usually be distributed over several fishing grounds, and the distribution of the fishing effort between these grounds is likely to depend on several factors other than the relative densities of the species concerned. These will include distance from port, shelter from bad weather, abundance of other species, and the market demand for one or other species, and some of these are likely to be variable. Thus the ratio of catch per unit effort to density is not likely to be constant.

However, from equation (3.1) we can for any fishing ground, i, whose area is A_i say, express the number of fish as

$$N_i = A_i D_i = \frac{Ai}{qi} \times \frac{Ci}{fi} .$$

If the whole range of the stock can be sub-divided into regions, within each of which equation (3.1) can be applied, then by adding, the total number in the stock is

$$N = \sum_i N_i = \sum \frac{Ai}{qi} \times \frac{Ci}{fi} .$$

If q_i is constant = q for all grounds, then

$$N = \frac{1}{q} \sum A_i \times \frac{Ci}{fi}$$

and density = $D = N/A = \frac{1}{q} \times \frac{1}{A} \times \sum A_i \times \frac{Ci}{fi}$ ..... (3.2)

where $A = \sum A_i$;

i.e. the density is the weighted mean of the catch per unit effort in each sub-region, the weighting factors being the areas of the regions. If all the areas are of equal size, this reduces to

$$D = \frac{1}{q} \sum \frac{Ci}{fi} .$$

The effective effort can be derived from equation (3.2) by dividing into the total catch,

i.e. $$f = \frac{C}{qD} = A \sum C_i \div \sum \frac{A_i C_i}{f_i} .$$

These formulae allow density indices to be obtained for any particular attribute in the population, e.g. an age-group. If the density index for the entire population is given by total catch divided by total effort, then the index for a given age-group is found by dividing the number landed of that age-group (see section on sampling) by the total effort. Otherwise the index is obtained by raising the number of each age in a unit weight by the weight caught per unit effort. If there are marked differences in composition between different regions of the stock, then the density indices will have to be obtained for each region separately, and the index for the whole stock obtained by weighting up by the areas of each region. The size of these regions should be small enough to ensure uniform composition within them, but in general should be larger than the separate grounds, which, as discussed earlier, are used in giving the overall density index.

The analysis of catch and effort data by small areas is particularly valuable when more than one species is being exploited, each species living in slightly different, but perhaps overlapping, parts of the whole fishing region. The proportion of a given species in the catch will therefore depend as much on where the catch was made, as on the abundance of that species. Within a sufficiently small sub-area, however, the proportion of a given species in the catch will be more nearly constant, and unaffected by the precise fishing position.

Another method of analysing fishing effort data on mixed species is possible when any one landing can be allocated according to the species which was the main objective of that trip - for example German trawlers fishing at West Greenland land during the year roughly equal quantities of cod and redfish. Any one landing, however, usually consists predominantly of cod or of redfish. The stock density of cod will then be estimated from the catch per unit effort of those trawlers fishing specifically for cod, and the density of redfish from the catches of those fishing for redfish. (Another method is discussed by Ketchen, in I.C.E.S. (in press)).

3.1 Exercises

1. Outline briefly the types of gear used in fisheries with which you are familiar.

2. What measures of effort are at present available?

3. What measures of effort would, ideally, be the best to use?

4. What are the possible causes of differences in fishing power, or fishing effort, between vessels or groups of vessels comprising the fleet?

5. Are there any reasons to suppose that, in any of these fisheries, the catch per unit effort is not proportional to the stock abundance; if so, can these be overcome by using a better measure of effort?

6. The table below is an extreme simplification of English North Sea trawl data and represents the effort and catches of plaice and haddock in two years. The area has been divided into sixteen sub-areas in each of which the data of catch and effort have been recorded separately.

	Year 1				Year 2			
Effort	5	6	6	3	16	17	13	14
Haddock	50	48	60	24	208	238	195	168
Plaice	0	12	6	0	0	17	13	0
Effort	8	7	9	8	13	12	13	10
Haddock	40	49	54	48	130	132	91	80
Plaice	16	0	27	8	13	12	26	0
Effort	10	13	11	14	9	9	(8)	6
Haddock	40	65	33	56	45	63	(32)	48
Plaice	40	39	22	42	18	18	(8)	18
Effort	14	15	16	15	5	5	6	4
Haddock	28	0	16	15	10	5	6	4
Plaice	84	90	48	45	25	15	12	8

(i) For each year obtain, by addition, total catch of each species and the total effort, and hence calculate the ratio total catch/total effort.

(ii) Draw up a chart for each year showing the catch per unit effort of each species in each rectangle.

(iii) Calculate for each species an overall density index, i.e. the mean catch per unit effort, and the effective overall fishing intensity on each species each year.

Compare the fishing intensities on the two species.
Compare the change in density between the two years as measured by the ratio total catch/total effort, and by mean c.p.e.

(iv) Supposing that there had been no fishing in the second year in one of the middle rectangles, as indicated by brackets in the table, how could mean density or effective overall fishing intensity be calculated? Make some reasonable assumption as to the density in the area; try the effect of different assumptions. Some assumptions are: that the density is the mean of surrounding areas; that the change from the previous year is the same as that for other areas; (as a limiting case) that the density is zero.

7. The table below gives the catch and effort statistics for the cod fishery in I.C.E.S. Region I (Barents Sea). The catches are given in tons (the total includes German and Norwegian catches), English fishing effort as millions of ton-hours, and Russian fishing effort as thousands of hours fishing. (Data from Arctic Fisheries Working Group Report).

Year	Catch			Effort	
	England	Russia	Total	England	Russia
1946	53,835	117,100	199,640	17.6	104
1947	127,242	151,970	340,758	38.4	149
1948	164,794	158,650	406,620	63.1	162
1949	226,450	162,340	484,942	80.0	171
1950	136,790	135,410	356,474	93.2	161
1951	129,030	189,580	407,989	98.9	231
1952	130,546	258,830	524,160	102.6	247
1953	59,445	261,400	442,839	53.1	275
1954	72,347	404,650	597,534	51.5	340
1955	91,379	530,280	830,694	60.6	373
1956	67,787	512,170	787,070	54.3	492
1957	38,488	183,000	399,595	44.5	-
1958	46,225	146,570	388,067	55.6	-

Calculate the total fishing effort in English and in Russian units.
Calculate the catch per unit effort of the English and Russian fleets.

Express each as a percentage of the 1946-56 average, and hence calculate pooled indices of catch per unit effort, and of total effort.

8. German trawlers fish at West Greenland for both cod and redfish. Their catches in tons and fishing efforts during 1958 and 1959 were as follows (data taken from I.C.N.A.F. Statistical Bulletins).

Year	Primary Species	Days Fished	Catch of Cod	Catch of Redfish
1958	Cod	1,337	26,247	1,754
	Redfish	385	1,277	9,457
	Mixed	199	2,386	1,969
	Total	1,921	29,910	13,170
1959	Cod	645	12,336	1,087
	Redfish	690	2,705	15,683
	Mixed	169	2,372	2,062
	Total	1,504	17,413	18,832

Estimate, from the catch per unit effort of cod by the trawlers fishing for cod, and of redfish by trawlers fishing for redfish, the changes (as percentages) in the densities of the stocks of cod and redfish between 1958 and 1959. Compare these with the changes in the catches per unit effort of cod and redfish by all vessels taken together, and also with the changes in the catches per unit effort of cod by the redfish vessels, and of redfish by the cod vessels.

4. MORTALITIES

4.1 Total Mortality

Before estimating the fishing and natural mortalities separately it is convenient to estimate the total mortality. This is readily done if we know the abundances, say N_o, N_1 of any group of fish at two known times, for then the fraction surviving is $N_1/N_o = S$, and the total mortality coefficient is given by

$$e^{-Zt} = S = N_1/N_o \qquad \text{..... (4.1)}$$

$$\text{or} \quad Zt = -\log N_1/N_o = \log N_o/N_1 \text{ where } t = \text{interval of time.}$$

This has the obvious special case where t = 1 year. The same formulae also hold when the true abundances are not known, but indices of them, e.g. catches per unit effort, are available, i.e. number n_o, n_1, proportional to N_o, N_1

$$\text{then } n_1/n_o = N_1/N_o = S$$

Often abundances, or indices of abundance, will not be known at any particular exact time, but only as averages over finite periods of time, e.g. a year. In terms of the abundance at the beginning of the period, N, and the total mortality coefficient, Z, the average abundance $\bar{N}$ during the period, duration t, is given by

$$\bar{N} = \frac{N}{tZ}\left(1 - e^{-Zt}\right)$$

If we denote by appropriate suffices the values of numbers and mortalities during periods 0 and 1 a year apart we have

$$\bar{N}_o = \frac{N_o}{Z_o t}\left(1 - e^{-Z_o t}\right)$$

$$\bar{N}_1 = \frac{N_1}{Z_1 t}\left(1 - e^{-Z_1 t}\right)$$

$$\text{and also} \quad N_1 = N_o e^{-Z_o}$$

Taking the ratio of the average abundances, we have

$$\bar{N}_1/\bar{N}_o = \frac{N_1}{Z_1}\left(1 - e^{-Z_1 t}\right) \Big/ \frac{N_o}{Z_o}\left(1 - e^{-Z_o t}\right)$$

$$\text{i.e.} \quad \bar{N}_1/\bar{N}_o = e^{-Z_o} \times \frac{Z_o}{Z_1} \times \frac{\left(1 - e^{-Z_1 t}\right)}{\left(1 - e^{-Z_o t}\right)} \qquad \text{..... (4.2)}$$

If $Z_o = Z_1$, then equation (4.2) reduces to

$$\bar{N}_1/\bar{N}_o = e^{-Z_o}; \quad \text{or } Z_o = \log_e \bar{N}_o/\bar{N}_1$$

i.e. the ratio of the mean abundances can be used in the same manner as the ratio of instantaneous abundances in equation (4.1).

The simplification can also be made if $Z_o t$ and $Z_1 t$ are both small, even if not equal, for then $1 - e^{-Z_1 t}$ is nearly equal to $Z_1 t$ and similarly for $1 - e^{-Z_o t}$. The ratio of the mean abundances during two periods therefore provides a good estimate of the survival if either the mortality is constant, or the change in numbers during both periods is small. Even if these conditions are not satisfied, the ratio may still provide a fair first approximation, subject to corrections which may be deduced from equation (4.2).

The formulae above will usually be applied to the abundances of individual year-classes and enable estimates to be made of the mortalities between any pair of successive years and for any fully recruited year-class. These estimates are likely to be quite numerous, and the question then arises as to how the "best" combined estimate of mortality can be obtained. A single combined estimate is only valid if there are no systematic differences in mortality, either with age or time, over the period considered; these may be most easily detected from an array such as Table 1, either by inspection of the means of rows and columns, or more rigorously by a statistical test, such as the analysis of variance.

Age	4/5	5/6	6/7	7/8	8/9	9+/10+	Mean
Years							
1950/1	0.75	0.80	0.65	0.70	0.55	0.75	0.70
1951/2	0.70	0.80	0.75	0.60	0.65	0.55	0.68
1952/3	0.65	0.60	0.85	0.70	0.85	0.70	0.72
1953/4	0.70	0.75	0.65	0.90	0.50	0.50	0.67
Mean	0.70	0.74	0.72	0.72	0.66	0.62	0.69

Table 4.1. Hypothetical example of estimated total instantaneous mortality coefficients for different pairs of year and age-groups

The entries in such a table should always be in the form of instantaneous coefficients, not percentage mortalities, as it is easy to show that the latter are biassed, being underestimated by an average amount depending on the variance of the data, and that this bias may be quite appreciable when taking the mean of several estimates. This bias is due to the numberator in equation (4.1) being not known exactly; the overestimate of the survival when the numerator is too low is greater than the underestimate when the numerator is, to the same extent, too high. A similar bias may be seen in comparing the mean of the reciprocals of a set of numbers, which is not the same as the reciprocal of their mean.

If there are no appreciable systematic differences between years or ages, then the entries in Table 4.1 can be considered as separate estimates of the same true mortality, and the combined estimate with least variance will be given by taking the weighted mean, with weights inversely proportional to the variances of the individual estimates. These variances will generally be unknown and though obviously the variance for the very old and scarce year-classes will be high, the present evidence (on limited data for plaice, herring and haddock) suggests that the variance is about constant for all the well represented age-groups (from IV to XI for the North Sea plaice). Thus, if the data for the older groups are combined (e.g. the last column of Table 4.1), all the variances will be nearly equal, and the appropriate overall estimate will be the simple mean of all the individual estimates. The mean estimate for the mortality for all ages between any one pair of years may be determined in the same way. Another common method for estimating the mortality between successive years is to take the decrease in the total numbers of all fully exploited year-classes, e.g. in Table 4.1, the ratio of 4+ to 5+. This is effectively weighting the estimates in Table 4.1 by the numbers of fish at each age.

The effect of using poor figures for effort and catch per unit effort, such that the latter does not bear a constant ratio to the true abundance, may be deduced from equation (4.1). Suppose the relation between catch per unit effort and abundance in the two years is given, with the obvious notation, by

$$n_1 = {}^{C_1}/_{g_1} = q_1 N_1; \quad n_2 = {}^{C_2}/_{g_2} = q_2 N_2.$$

Then $\quad {}^{n_2}/_{n_1} = q_2 N_2 / q_1 N_1$

If $N_2 = N_1 e^{-Z}$ then

$$\log_e {}^{n_1}/n_2 = \log_e {}^{q_1}/q_2 + Z \qquad \text{.....} \quad (4.3)$$

Thus the estimated mortalities will include an extra term, equal to the logarithm of the change in q (the "availability" or "catchability coefficient"). A change in q will show, in an array such as Table 4.1, as a year-to-year change in mortality unconnected with changes in fishing or other causes of mortality.

Data on the abundance of successive ages in catches made at any one time - e.g. in one year - can be used in a similar way. Taking t_c as the age at which fish enter the fishery, at which times the numbers of two successive year-classes are N_o, N'_o, then their abundances at the time of sampling when they are aged t + 1 and t will be

$$N_{t+1} = N_o e^{-Z(t+1-t_c)}$$

$$N_t = N'_o e^{-Z(t-t_c)}$$

$$\therefore \log_e {}^{N_t}/N_{t+1} = \log {}^{N'_o}/N_o + Z \qquad \text{.....} \quad (4.4)$$

In equation (4.2) catch per unit effort, or even percentage age data, can be used as indices of abundance directly in the equation, for the coefficient q, related to availability, in the top and bottom of the ratio, relates to the same period, and therefore cancels out, viz.

$$\log_e {}^{n_t}/n_{t+1} = \log_e {}^{qN_t}/qN_{t+1} = \log {}^{N'_o}/N_o + Z \qquad \text{.....} \quad (4.5)$$

Equations (4.3) and (4.5) are very similar, both containing a term additional to the true mortality. Ratios of catch per unit effort of the same year-class (i.e. equation (4.3) are best to use when year-class strength is variable, or when "availability" changes are small and effort is readily measured. Equation (4.5) is better when measurement of effort is difficult, or year-class variation is small, and also when data are available only for isolated years. A disadvantage of equation (4.5) is that it does not measure the contemporary situation - the additional mortality undergone by the older of two adjacent age-groups is that which it underwent during its first year in the fishery - later mortalities have been applied to both year-classes equally.

Estimates of total mortality over a period can also be obtained by semigraphical methods. If Z (the total mortality) is constant we can give the numbers of a year-class at any time, t, after it is subject to the full mortality, as

$$N_t = N_o e^{-Zt}$$

where N_o = numbers at time t = o

$$\therefore \log_e N_t = \log_e N_o - Zt.$$

If now $\log_e N_t$ is plotted against t, it will give a straight line of slop -Z. This plot can be made either for the catch per unit of a single year-class at different times, in which case deviations, other than sampling variance, will be caused by changes in "availability", or for numbers of different year-classes at the same time - the well known "catch-curve". (A detailed analysis of such curves, including the interpretation of non-linear catch-curves is given by Ricker, 1958). Deviations will be caused in the catch-curve by inequalities in original year-class strength, but the value of the "availability" in the year of sampling will alter only the position of the curve, and not its slope, or the scatter of the points. This graphical method can also (and probably most easily), be used by plotting N_t against t on semi-logarithmic paper. This should give a straight line, from which the mortality is best estimated as follows. Note where the line has some convenient value (say 100), find the value on the line exactly one year later (equals say 65). Then the survival through one year = $^{65}/_{100} = e^{-Z}$ from which Z can be at once locked up in suitable tables.

All the above methods, when applied to age-composition of catches, are subject to bias when the different ages are not equally vulnerable to the gear used. If the vulnerabilities of successive ages, t, t+1 are ${}_tq$, ${}_{t+1}q$ so that the catches, or catches per unit effort, are given by

$$n_t = {}_tq.N_t$$

$$n_{t+1} = {}_{t+1}q \cdot N_{t+1}$$

$$\log_e {}^{n_t}/_{n_{t+1}} = \log_e {}^{tq}/_{t+1}q + \log_e {}^{N_t}/_{N_{t+1}}$$

$$= \log_e {}^{tq}/_{t+1}q + Z$$

In practice this type of bias may be difficult to detect, unless there are abrupt changes with age, when the apparent mortality will also change with age, though the possibility of its existence should never be neglected. Because such differential vulnerability by age implies that fishing mortality is different for each age, the forms of the true age-distribution and of the apparent age-distribution may be quite complicated (see Jones, in press). Sometimes, e.g. when decreased vulnerability is balanced by decreased mortality, the age-distribution of the catches may be very similar to that obtained with constant mortality.

Total mortality can also be estimated from the "virtual population". The virtual population of a certain year-class on say its eighth birthday is the total number of fish of that year-class caught after their eighth birthday.

The mortality during the ninth year of life is then obtained as the logarithm of the ratio of the virtual populations at nine and at eight years old. The method is probably most useful for long-lived fish, of which fishing takes a major share, but for which "availability" varies and is difficult to measure. (see Fry, 1957; Bishop, 1959).

When the age-composition is not known, estimates, and sometimes quite good estimates, of total mortality can be obtained from length data. The relative number of fish in two different size groups will depend on (1) the time taken to grow from one size to the other; (2) the mortality rate during that period; and (3) the time taken to grow through each size-group, i.e. the proportion each size-group is of a complete year-class. These factors have one particularly simple case if there is a range of sizes over which the growth is linear, or approximately so. Then if the numbers in each size-group are plotted on a logarithmic scale, as for a "catch-curve", the plot should yield a straight line, whose slope is proportional to the total mortality coefficient. Further, if the growth rate is known, the absolute value of the mortality can be determined.

The total mortality can also be measured in a steady state by the average age or length in the exploited population, which will, if the fishery is not selective, be the same as that in the catch. If the ages and lengths of entry into the exploited phase, and the averages in the catch, are t_c, l_c, $\bar{t}$, $\bar{l}$ respectively, the following expressions for Z can be readily derived (c.f. Beverton and Holt, 1956).

$$Z = \frac{1}{\bar{t} - t_c} \quad ; \quad Z = \frac{K(L_\infty - \bar{l})}{\bar{l} - l_c}$$

where K, L_∞ are the constants in the Bertalanffy equation.

4.2 Fishing Mortality

There are numerous methods for estimating the fishing mortality, none of which is entirely satisfactory, and in practice it is advisable to obtain estimates from as many independent methods as possible. The main methods are outlined here, dealing first with the more direct ones.

1. Direct census. If the total stock is known, the fishing mortality can be calculated at once from the catch. The total numbers may be obtained by a complete or sample count, e.g. salmon passing upstream, or whales seen in a known area; usually, the only practicable method for marine fishes is the census of adult females by counting, by a suitable plankton survey, the number of eggs produced. The total numbers are then estimated from the proportion of adult females in the catch and their fecundity. An advantage is that it is rather easier than with most other methods to

attach statistical confidence limits to the estimates, though these may be wide (see English, in press).

2. "Swept Area". From the definition of the instantaneous mortality coefficient it follows that the fishing mortality generated by a single operation, which may be considered as taking an infini--tesimally small part of the whole stock, is equal to the fraction of the population which is caught. If the stock is evenly distributed and the gear effectively catches all the fish within a certain area, a, and the total area inhabited by the stock = A, then the fishing mortality coefficient is equal to $^{a}/A$. The mortality generated by the whole fishery is then a'/A, where a' is the sum of the areas covered by all the vessels of the whole fleet.

This method is, of course, confined to gear for which the area covered can be readily estimated, e.g. for a trawl haul the area covered would appear to be the distance between the doors times the distance covered. There are two important sources of error, acting in opposite directions. First, since some of the fish in the area covered by the gear may escape, the method may over-estimate the mortality. Secondly, as mentioned in the section on effort, the density of fish in the fished area will be greater than the average density, leading to an underestimate of the fishing mortality. The method therefore cannot give an exact estimate of fishing mortality, but may sometimes be useful to give an indication of its order of magnitude. In particular, it is often useful in showing whether fishing is likely to be having a significant effect. The method may also be used where the area covered by fish can be determined from an echo survey. (For uses of echo-sounders, etc in measuring abundance, and hence fishing mortality, see the I.C.E.S. Symposium on the measurement of fish abundance, especially papers by Cushing, and Fedorov).

3. Marking. Marking experiments are, of course, one of the best known methods of estimating the fishing mortality. If the population of marked fish is in all ways the same as the total stock, the fishing mortality is readily determined from the number of marked fish returned, e.g. the number caught in the first complete year after liberation is given by

$$n = \frac{FN}{F + M}\left(1 - e^{-F+M}\right);$$

where N = number of marked fish liberated.

The total mortality coefficient Z (=F+M) may be determined from marking returns, e.g. as the natural logarithm of ratio of numbers caught in the second year to those in the first. Unfortunately the assumptions necessary for the simple theory to work are rarely satisfied in marine fisheries, and the use of marking data requires somewhat more elaborate methods. These are discussed in the next section.

4. Changes in total mortality. If the amount of fishing changes, thus changing the fishing mortality, this will result in a change in total mortality. Thus if observed changes in the latter can be related quantitatively to known changes in fishing effort, the value of the fishing mortality coefficient at any given level of effort can be deduced. Mathematically, we have

$$Z = F + M = q\,f + M \qquad \text{.....} \quad (4.6)$$

If a series of pairs of values of f (fishing effort) and Z (total mortality coefficient) are known, equation (4.6) gives a linear relation between them. For two such pairs this gives two simultaneous equations which can be solved for q and M. For more than two pairs the plot of Z against f should yield a straight line, slope q and intercept on the axis M. The solution for q and M can be obtained by the normal regression techniques of statistics, for equation (4.6) is in the standard form for a linear regression

$$y = a + bx$$

where y = total mortality coefficient: x = fishing effort.

Denoting by $\bar{x}$, $\bar{y}$ the mean values of x and y, the least squares estimates for M and q are

$$q = b = \frac{\Sigma(x-\bar{x})\ (y-\bar{y})}{\Sigma(x-\bar{x})^2} \qquad \text{.....} \quad (4.7)$$

$$M = a = \bar{y} - b\,\bar{x} \qquad \text{.....} \quad (4.8)$$

The test as to whether b is in the statistical sense significantly different from zero, i.e. whether q is different from zero, and hence whether fishing is having a measurable effect, is the same as the usual test for the significance of the correlation coefficient r. This is given in most statistical tables for a set of values for the number of degrees of freedom, equal to two less than the number of pairs of observations. The value of r may be calculated from the equation

$$r = \frac{\Sigma(x - \bar{x})\ (y - \bar{y})}{\sqrt{\Sigma(x - \bar{x})^2 \Sigma(y - \bar{y})^2}} \qquad \ldots\ldots\ldots\ldots\ldots\ldots (4.9)$$

To test whether q, and hence F, is different from zero is not the only test, and perhaps not even the most useful, since in practice F must have a non-zero value even if small. To establish certain confidence limits within which F almost certainly lies is generally more useful. Confidence limits for M and q are deducible from equations (4.8) and (4.9). For if

S^2 = variance of y about the regression line

S^2 is given by the equation:

$$(n - 2)\ S^2 = \Sigma(y - \bar{y})^2 - b\ \Sigma(x - \bar{x})\ (y - \bar{y}) \ldots\ldots\ldots\ldots (4.10)$$

n being the number of pairs of observations,

$$\text{variance of } M = S_M^2 = S^2\left(\frac{1}{n} + \frac{\bar{x}^2}{\Sigma(x - \bar{x})^2}\right)$$

$$\text{and variance of } q = S_q^2 = S^2\left(\frac{1}{\Sigma(x - \bar{x})^2}\right)$$

The 5% confidence limits for M and q are therefore $a \pm 2\ S_M$; $b \pm 2\ S_q$ respectively. The calculations involved in these equations may be simplified by using the right hand expressions in the equations below

$$\Sigma(x - \bar{x})^2 = \Sigma x^2 - n\bar{x}^2 = \Sigma x^2 - \bar{x}\Sigma x = \Sigma x^2 - {}^1/n\ (\Sigma x)^2$$

$$\Sigma(y - \bar{y})^2 = \Sigma y^2 - n\bar{y}^2 = \Sigma y^2 - \bar{y}\Sigma y = \Sigma y^2 - {}^1/n\ (\Sigma y)^2$$

$$\Sigma\ (x - \bar{x})\ (y - \bar{y}) = \Sigma xy - n\bar{x}\bar{y} = \Sigma\ x\ y - \bar{x}\ \Sigma\ y = \Sigma\ xy - {}^1/n\ \Sigma\ x\ \Sigma\ y$$

If the mortalities used in the regression have been estimated from indices of abundance at known instants in time, i.e. from equation (4.1), the results of the regression can be used at once. Thus the mortality between 1st January, 1961 and 1st January, 1962 can be related to the total fishing effort in 1961. More usually the indices of abundance will be known only as averages over a period - e.g. as the mean catches per unit effort in 1961 and in 1962. As equation (4.2) shows, the mortality estimated from the ratio of the two indices of abundance (i.e. $\log \bar{N}_1/\bar{N}_o$) will be related to the mortalities (and hence fishing effort) in both periods. The mortality should therefore be related to the average of the total fishing effort in the two periods. Thus, for example, graphically we would plot the log ratio of the mean numbers in 1961 and 1962 against the average effort in 1961 and 1962. It can be shown that this method does in fact make the most efficient use of the data (Paloheimo, 1961).

This method, though most obviously used for effort varying with time, i.e. from year to year, can also be applied when the fishing effort varies with age, supposing that a selective gear is in commercial use, but that true density indices of each age-group can be obtained, e.g. by special research vessel sampling.

When the estimates of mortality between successive pairs of years are highly variable, because of sampling errors or other causes (e.g. changes in "availability") rather than real changes in mortality, an average mortality coefficient over several years can be obtained by following the fortunes of a single year-class throughout its life in the exploited phase. If its density index is plotted on a logarithmic scale this should yield a straight line, slope equal to the mortality coefficient, and this last can be plotted against the average fishing effort in the corresponding period. Though this method gains in reducing the scatter, this is at the cost of losing information on the effect of year-to-year changes, though not of long-term trends, in fishing effort. Also, since the data for adjacent year classes come to a large extent from the same years, the points are not fully independent, and the exact tests of significance and confidence levels, outlined above, also cannot be applied.

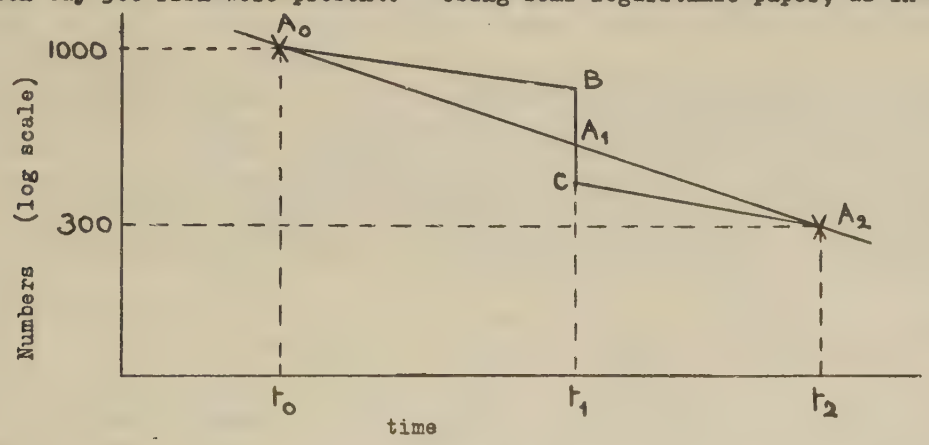
4.3 Natural Mortality and Growth Characters

An idea of the value of the natural mortality rate can be gauged from the growth pattern of the species concerned. A fish which approaches its ultimate length quickly - i.e. has a high value of K - is likely to have a high natural mortality, whereas a fish that grows slowly (a low K) is likely also to have a low M. The relation between M and K appears to differ from one group of fish to another - thus for clupeoids M = 1.5 K, for gadiforms M = 2.5 K. Like the "swept area" method for estimating fishing mortality this is not a precise method, but is often most useful in the early stages of studying a fishery in judging whether natural (or fishing) mortality is likely to be the dominant element in the total mortality (Beverton and Holt, 1961).

4.4 Special Graphical Methods

Graphical methods can also be used to estimate mortality rates from some other special situations where algebraic methods would be difficult. Regier (1962) has described some such situations where census data giving the stock in absolute numbers at different times are available, and also statistics of total catch, either during a very short season (perhaps only a few days, so that fishing mortality is extremely high), or during a season covering only a part of the period between the two census dates.

Consider first a very short fishing season, during which 300 fish are caught in, say, two days. At some time, t_o, before the season say 1000 fish were present, and at some time t_2 after the season say 300 fish were present. Using semi-logarithmic paper, as in the figure below,



the population sizes at the two census dates are given by points A_o, A_2. If the mortality rates had been constant the population at the time of the fishing season, t_1, would have been A_1. In fact the real changes in the population would be described by the line A_oBCA_2 in the figure where BC represents the catch of 300 fish, and the two parallel lines A_oB, CA_2 the decrease due to natural mortality. As the two triangles A_oBA_1, A_1CA_2 are similar the ratio of the lengths $BA_1 : A_1C$ (as measured by a ruler on the semi-log paper) will be equal to the ratio of the periods $(t_1-t_o):(t_2-t_1)$. As a first approximation take some position of C and the position B at a value of C + 300. Measure with a ruler the distance BC (this distance will vary with the value of C). Then the distance CA_1 as measured with a ruler should be equal to $BC(t_2-t_1)/(t_2-t_o)$. If it is greater than this the first approximation of C is too low; the correct value of C can thus quickly be found. The natural mortality is then readily determined from the line A_oB (or CA_2) - as usual this is most easily done by noting where it crosses the population size of 1, or 100 etc., and reading off the population size exactly one year later.

More generally, fishing takes place over a period - the open season - during which the fishing mortality can be taken as constant. Censuses are made at two times outside the fishing season, so that the time between the two censuses include two periods before and after the open season during which only natural mortality is occurring. As a first approximation the known catch, C, may be assumed all to be taken at the midpoint of the season, and using the method described above a first estimate of natural mortality, M_1, can be obtained. Using this value of M the deaths outside the fishing season can be calculated and hence, by subtraction, the total deaths N, and the total mortality Zt (where t = duration of season) estimated.

Then F may be estimated from

$$Ft = Zt \times {}^{C}/_{N}.$$

A second estimate of natural mortality, M_2 can be obtained by

$$M_2t^1 + Ft = -\log {}^{N_1}/_{N_2}$$

where N_1, N_2 are the numbers at the time of the two censuses, and t^1 the time between censuses. A better estimate of M is $M_3 = \frac{1}{2}(M_1 + M_2)$, which can be used in further iterations to obtain improved estimates of F and M.

4.5 Exercises

1. A research vessel in five one-hour trawl hauls caught the following numbers of fish at each age

   I, 30; II, 450; III, 120; IV, 70; V, 25; VI+, 15

   A year later, the catches in twelve one-hour hauls were

   I, 60; II, 960; III, 480; IV, 120; V, 72; VI+, 42

   Assuming that, with the mesh size in use, the catch per hour gives a valid index of density for two-year old fish and older, estimate the total mortality coefficient during the year. If the only data available were those for the first of these years, give an estimate of the average total mortality during the previous few years.

2. A group of fish is subject in two successive years to total mortality coefficients of 0.85 and 0.80. If the number present at the beginning of the first year is 1,000 what is the average number present in each of the two years?
   What is the total mortality coefficient estimated from these two averages?

3. A plankton survey showed that 2×10^{11} eggs were laid during a spawning season.
   Fecundity studies showed that the average mature female laid 10^5 eggs.
   Market studies showed that 3,000,000 fish were landed during the year following, and of these 40% were mature females (i.e. had spawned at least once).

   What percentage of the spawning females was caught during the year? If the total mortality coefficient was 1.2, what were the fishing and natural mortality coefficients?

4. When shot, the warps of a seine-net form approximately a circle of circumference 4,000 metres. If 100,000 hauls were made in a certain year in the North Sea, for which the area inhabited by plaice is approximately 200,000 sq km, give a rough estimate of the value of mortality coefficient of the plaice population caused by fishing by seine.
   On what assumption is this estimate based?

5. The average number of plaice landed at Lowestoft per 100 hours' fishing in two periods were

Age	2	3	4	5	6	7	8	9	10
1929-38	125	1,355	2,352	1,761	786	339	159	70	28
1950-58	98	959	1,919	1,670	951	548	316	180	105

   Calculate the average total mortality coefficients in the two periods. If the average total fishing efforts on plaice in the North Sea during the two periods were, in terms of millions of hours fishing by English steam trawlers, 5.0 in 1929-38, and 3.4 in 1950-58, estimate from equation (4.6) the natural mortality, and the fishing mortality in the two periods.

6. The table below gives the age-composition of cod in terms of numbers landed per 100 ton-hours fishing by English trawlers, in the Barents Sea, and the total fishing effort in each year.

Year \ Age	3	4	5	6	7	8	9	10	11	12+	Effort
1932	0.02	0.38	1.49	3.16	3.81	2.16	1.55	2.20	1.48	2.80	174
1933	-	0.37	2.12	3.37	4.62	3.37	1.60	1.37	0.64	2.18	184
1934	-	0.43	3.18	6.18	5.47	8.69	2.59	0.75	0.56	1.98	164
1935	0.03	0.56	7.85	13.97	10.04	5.82	2.82	0.88	0.29	1.22	184
1936	0.1	0.58	1.75	8.61	7.96	9.28	3.50	0.93	0.19	1.13	252
1937	0.02	1.89	2.91	7.66	17.05	8.65	2.53	0.38	0.26	0.33	321
1938	0.4	1.87	7.09	5.73	9.46	9.54	4.30	1.24	0.48	0.13	253
1946	7.3	11.52	11.39	18.91	13.77	11.77	14.29	17.65	5.26	3.13	66
1947	2.1	18.25	28.42	28.42	22.57	5.99	7.10	10.45	11.01	4.74	103
1948	0.9	1.89	15.59	33.19	46.77	11.31	7.17	2.01	3.65	2.76	156
1949	4.4	12.92	18.38	34.83	20.08	9.08	6.58	2.94	1.59	2.50	171
1950	-	0.49	1.15	5.49	12.89	9.32	4.28	1.76	1.01	0.37	248
1951	0.04	1.41	8.61	13.58	11.52	6.62	4.11	1.76	1.96	0.02	313
1952	0.15	4.65	11.84	16.26	13.14	4.09	2.11	1.52	0.91	0.93	412
1953	0.02	2.02	13.77	16.41	7.20	5.49	1.62	0.70	0.15	0.25	396
1954	0.07	5.33	19.03	21.76	10.25	3.99	1.62	0.48	0.67	0.13	425
1955	-	0.73	10.83	26.82	15.70	5.44	1.93	1.30	0.57	0.19	551
1956	0.02	0.50	6.29	22.76	13.51	5.59	1.20	0.61	0.24	0.08	630
1957	0.08	1.98	3.40	9.81	9.70	6.55	1.29	0.58	0.38	0.10	457
1958	0.6	4.4	9.98	8.31	5.81	5.53	1.56	0.91	0.42	0.20	414

Tabulate the total mortality for each pair of years for each age. Examine the data and decide from what age the fish are fully represented in the catches. Hence obtain a single estimate for the mortality between successive pairs of years (take the ratio 7 and older: 8 and older, or mean of the mortalities for each age). By relating this mortality graphically and by calculation of the regression line to the average fishing effort in the two years, estimate the natural mortality and the fishing mortality in 1958.
What are the confidence limits to the natural mortality?

5. TAGGING

Tagging of fish can be used in studying growth, and movements and migration. This section, however, is concerned only with the use of tagging data to determine the mortality rates of the population, and the size of the population. (Growth is referred to in Section 2). The simplest assumption is that the tagged fish are subject to constant fishing and natural mortality rates which are the same as in the natural untagged population, and these can be estimated separately, because, unlike the natural population, the initial number in the tagged population is known precisely.

That is, if N_o fish are tagged, the number N_t alive after time t is given by

$$N_t = N_o e^{-(F + M)t} \qquad \text{..... (5.1)}$$

and if the returns are grouped in time intervals of length t, the number n_r caught during the rth interval between times rt, (r + 1)t is

$$n_r = N_o e^{-(F + M)rt} \frac{F}{F + M} \left(1 - e^{-(F + M)t}\right) \qquad \text{..... (5.2)}$$

(Note: The first interval after tagging is r = o).

The numbers caught in successive intervals can therefore be used, knowing N_o, to give estimates of F and M. In particular,

$$\log n_r = -(F + M)tr + \log \frac{FN_o}{F+M} \left(1 - e^{-(F + M)t}\right) \qquad \text{..... (5.3)}$$

so that if log n_r is plotted against r, the result is a straight line, slope -(F+M)t. (An alternative, and rather more convenient form of this equation is given in equation 5.9). Using this value of (F+M), F can be estimated from the numbers returned in any interval, using equation (5.2), or from the intercept on the y-axis, which from equation (5.3) is

$$\log \frac{FN_o}{F+M} \left(1-e^{-(F+M)t}\right)$$

Alternatively, the total number of returns up to time T is

$$\frac{FN_o}{F+M} \left(1-e^{-(F+M)T}\right)$$

from which, substituting for F+M, a direct estimate of F can be obtained. When T is very large this reduces to $\frac{FN_o}{F+M}$.

Unfortunately the assumptions made on this simple example are not often fulfilled. The types of errors which may arise can be placed in definite groups, according to their effect on the various estimates.

1. Errors which affect the estimate of the rate of fishing (F), but not the estimate of total mortality (Ricker's type A, Beverton and Holt's type 1);

   (a) death of fish immediately after tagging;
   (b) incomplete reporting of tags recaptured by fishermen (assuming the proportion not reported stays constant).

2. Errors which affect the estimate of the total mortality, but not that of fishing (Ricker's type B, Beverton and Holt's type 2);

   (c) loss of tags from fish which occurs at a steady instantaneous rate throughout the experiment;

   (d) additional mortality of tagged fish, also occurring throughout the experiment;
   (e) emigration of tagged fish.

3. Errors affecting estimates of both fishing and total mortality;

3. Errors affecting estimates of both fishing and total mortality;

(f) tagged and untagged fish not equally vulnerable to fishing, e.g. the additional likelihood of fish tagged with Petersen discs to be retained by a net;

(g) tagged fish not uniformly mixed with the untagged population.

Type 1 errors will lead to an underestimate of the true fishing mortality, which in itself may often be useful. They can often be detected and possibly measured by suitable observations. Thus in suitable conditions tagged fish can be kept in tanks or cages and their mortality for the period after tagging can be directly observed. Less directly the percentage returns of fish which when tagged were in different conditions - lively or not so lively, damaged or apparently undamaged, etc, or captured by different methods - can be compared. If there is any mortality due to the shock of capture and tagging then it will presumably be lower for lively fish, and higher for bruised or damaged fish (loss of scales often appears to be particularly critical). Absence of such difference can be taken as an indication, though not proof, of little or no such mortality.

Non-reporting of tags can often be detected by comparing the number of tags returned per unit quantity of fish caught by various groups of vessels fishing in the tagging area - individual boats, different countries, etc. It may be directly measured by feeding known numbers of tagged fish into the catches; this is general practice with mechanical methods of recovery (e.g. magnets at fish meal factories), but can, particularly with the co-operation of a few fishermen, be used for normal external tags returned by fishermen or shore workers.

Type 2 losses can be considered as an additional cause of mortality, so that equation (1) should be written as

$$N_t = N_o e^{-(F+X)t} \qquad \text{..... (5.4)}$$

where X includes all causes of reduction of tagged fish other than fishing - loss of tags and emigration as well as natural mortality. Equation (5.4), and the corresponding form of equation (5.2)

$$n_r = N_o e^{-(F+X)tr} \frac{F}{F+X} \left(1 - e^{-(F+X)t}\right) \qquad \text{..... (5.5)}$$

will be the usual form for analysis of tagging data, so that in fact only the fishing mortality of the natural population will be estimated from tagging. Natural mortality will be given by subtraction from the total mortality, Z, estimated from age-composition, etc.

Some quantitative estimate of type 2 losses can sometimes be obtained, for instance losses of tags (but not mortality of tagged fish) can be estimated by attaching two tags to each fish and noting the proportion of fish returned with both tags, and with only one tag, and the change in this proportion with time.

Differential vulnerability to fishing of tagged fish can usually be eliminated by suitable design of tags. Fish carrying button type tags are likely to be particularly vulnerable to certain types of gear - e.g. set nets - and if possible such tags should not be employed where this type of gear is used, but if they have to be used, or in order to interpret past data, the extent of the extra fishing mortality can be gauged by comparing the rate of return of fish with different types of tags.

Non-uniform distribution of tagged fish is likely to present one of the major problems. If mixing is relatively quick, returns during some initial period, 0 to t', during which the tagged fish are mixing with the untagged population, may be omitted in the computations. The analysis is then carried on from time t', with a reduced initial number of tags, using equation (5.1) in the form

$$N_t = N_o' e^{-(F+X)(t-t')} \qquad \text{..... (5.6)}$$

N_o' is estimated from the number tagged, subtracting the number returned in the initial period of mixing, and the estimated number lost through other causes, X. This last estimate will have to come from an analysis of the later data. However, in many situations nearly all returns will be made before the tagged and untagged populations are even approximately mixed.

This mixing may be effectively speeded up by a suitable pattern of tagging. The aim is to have the ratio of tagged to untagged fish the same throughout the population. This might for instance be achieved by making an evenly spaced grid of trawl stations covering the whole area, and tagging all, or a constant proportion of, the fish caught at each station. This is possible in a small area, but not easy to do in, say, the North Sea.

In a large area such as the North Sea it is usually necessary to use data on the detailed distribution of fishing effort. From these the rate of return of tagged fish can be related to the fishing intensity in the tagging area, and hence an estimate obtained of the coefficient q in the equation $F = qf$. This can then be applied to the fishing intensity on the population as a whole to give the fishing mortality of the population.

Consider a small area around the position of tagging in which mixing of tagged and untagged fish takes place quickly. For a certain time interval, i, let

$\bar{N}_i$ = mean number of tagged fish present

f_i = fishing intensity (effort per unit area)

n_i = number of tagged fish returned.

Then $$n_i/f_i = q\,\bar{N}_i \qquad \text{..... (5.7)}$$

If then n_i/f_i, the tags returned per unit fishing intensity, is plotted against time, and a curve fitted to the points, the intercept of this curve on the y-axis will be qN_o, where N_o is the number released. Hence q can be estimated and the fishing mortality on the population as a whole will be given by

$$F = q\tilde{f}$$

where $\tilde{f}$ is the effective overall fishing intensity on the population, as calculated from detailed effort statistics.

While these following assumptions may not be completely justified, to a first approximation, the fishing intensity within the small area chosen around the release point may be taken as constant, and the movement out of this area defined by a constant exponential coefficient, D, and therefore the number of tagged fish in the area after time t, N_t, will be given by

$$N_t = N_o\, e^{-(F + X + D)t}$$

where F is the fishing mortality occurring in the area round the release point, and not necessarily that in the population as a whole. If the ith interval is of duration t, and extends from time $(i - \frac{1}{2})t$ to $(i + \frac{1}{2})t$

$$\bar{N}_i = N_o\, e^{-(F + X + D)(i - \frac{1}{2})t} \left[1 - e^{-(F + X + D)t}\right] \frac{1}{(F + X + D)t}$$

$$\text{or} \quad \bar{N}_i = N_o\, e^{-(F + X + D)it} \left[\frac{e^{\frac{1}{2}(F + X + D)t} - e^{-\frac{1}{2}(F + X + D)t}}{(F + X + D)t}\right] \qquad \text{..... (5.8)}$$

Thus, so long as $(F + X + D)$ is small, i.e. the numbers do not change very greatly during one interval, to a close approximation the term in the brackets will be equal to unity

$$\bar{N}_i = N_o\, e^{-(F + X + D)it} \qquad \text{..... (5.8')}$$

and the plot of n_i/f_i against time should be a straight line if plotted on a logarithmic scale. It may be noted that equation (5.8), and particularly its approximate form (5.8') suggests a good alternative to equation (5.3) in the form

$$\log n_r = -(F + M)(r + \tfrac{1}{2})t + \log FN_o t + \log \left[\frac{e^{+\frac{1}{2}(F + M)t} - e^{-\frac{1}{2}(F + M)t}}{(F + M)t}\right] \qquad \text{.... (5.9)}$$

where again the last term may be neglected if the change in numbers during the interval is small, i.e. if the logarithm of numbers recaptured during each interval are plotted against the mid-point of the interval, then the plot should be a straight line, slope $-(F + M)$, and intercept on the axis $\log FN_o t$.

Equation (5.7) can be extended to cover data from more than one small area round the release point. Denoting values for particular areas by prefixes

$$\bar{N}_i = \Sigma\, {}_j\bar{N}_i$$

when $\bar{N}_i$ = total of tagged fish in the areas being analysed

$_j\bar{N}_i$ = number of tagged fish in the jth area.

$q\,_j\bar{N}_i = {}_jn_i/{}_jf_i$

and therefore $\Sigma\, {}_jn_i/{}_jf_i = q\Sigma\, {}_j\bar{N}_i = q\bar{N}_i$ ..... (5.10)

so that the analysis can be carried out as before, using the sum of the tags returned per unit fishing intensity in each small area. The analysis can be carried out only when sufficient effort data are available; if tags are returned from a mixed fleet, some of which provide adequate effort data and some of which do not, then in all the analysis only data from the fleet or fleets providing complete data both of effort and tags returned should be used. Tagged fish caught by the other fleet are considered as other losses. Data from the other fleet are brought into the considerations only at the end, when computing the fishing mortality on the population as a whole.

5.1 Exercises

1. Graham (1938) tagged 1,000 cod in the North Sea, and the following numbers were returned, grouped in three monthly intervals.

Months	0-2	3-5	6-8	9-11
Numbers	139	91	52	40

By plotting the logarithm of the numbers returned against time, estimate the total and fishing mortality coefficients. (Compare the results of using equation (5.3) and the approximate form of equation (5.9).

2. Whiting tagged and released in the Irish Sea were graded according to their liveliness and the damage to their scales, and the numbers released, and subsequently recaptured were as follows (data from Beverton and Bedford, 1962).

Condition	Scales	Number tagged	Number returned
Lively	Good	60	18
"	Moderate	98	21
"	Poor	49	6
Sluggish	Good	254	60
"	Moderate	765	159
"	Poor	509	43

What evidence is there of mortality at tagging? Assuming all the best quality fish survived, what proportion of each other category died, and what was the effective number released?

3. From cod tagged in the Gulf of St. Lawrence in 1955, the following numbers were returned by different countries in 1956 (from Dickie, 1962).

Country	Number of Tags	Total Cod Landings (tons)
Canada	392	62,400
France	32	28,000
Portugal	29	5,800
Spain	15	8,100

Calculate the number of tags returned per 1,000 tons of fish landed by each country. What evidence is there of incomplete returns? If all tags recaptured by Canadian fishermen are returned, estimate the number actually recaptured by other countries.

4. Three groups of herring tagged with internal tags were released in the North Sea in the summer of 1957. Detailed data of Danish fishing effort in the areas round the release points were available, in terms of hours' fishing per statistical square (15 x 15 miles). The number of tags returned, and the fishing intensity round each tagging position in the weeks following tagging, were as follows (data adapted from ICES, 1961).

Week After Tagging	Liberation Number					
	1		2		3	
	Tags	Intensity	Tags	Intensity	Tags	Intensity
1	21	80	80	420	3	10
2	35	64	12	60	3	5
3	30	53	10	50	8	15
4	8	26	2	10	2	10
5	10	56	1	10	-	-
Number Tagged	3,000		1,500		3,000	

Plot the tags returned per hours fishing per square for each liberation. Hence, if the efficiency of the recovery technique is such that 90% of the tags caught are returned, what is the value of q, the mortality caused by an intensity of 100 hours fishing per square?

6. RECRUITMENT AND SELECTION

Not all sizes or ages of fish undergo the same fishing mortality: small fishes may escape through the meshes of a net, or not be in the main fished area. It is useful to distinguish the part due purely to behaviour (in the widest sense) of the fish themselves - recruitment - and that due to the properties of the gear selection.

Recruitment is the process in which young fish enter the exploited area and become liable to contact with the fishing gear. This may involve an actual movement, as in the North Sea plaice, which moves, when relatively old (about three to four years), from the shallow nursery area along the coast into the main fishing grounds. Recruitment may involve only a change in habit, such as in the North Sea haddock, where young and old occur in the same areas, with the very young fish being pelagic, and recruiting to the exploited phase when they take up a demersal habitat in the autumn of their first year of life. Mathematically, the important quantity is t_r = mean age at recruitment.

6.1 Trawl selection

Selection is simplest in the bag-type of gear - trawls, seines etc. For these gears it is usual to assume that the size composition of the fish entering the mouth of the net is the same as that in the immediate vicinity of the gear. The selectivity of such gears therefore becomes a question of escape, through the meshes, of fish which have entered the net. For many species there is evidence to show that most of this escape occurs through the cod-end. Selectivity can therefore be determined directly if the numbers of each size of fish entering the net can be estimated, either by attaching a small-meshed cover over the cod-end or other parts, or from the size-composition of the catches of nets of much smaller meshes fished at the same time and place. Whichever method is used, the results can be expressed as the proportion of fish at each length entering the net which are retained in the cod-end. When these proportions are plotted against length, the selection curve of the net for the species concerned is obtained. A typical example is shown in Fig. 1.

A selection curve may extend over a range of length of fish of perhaps 10 cm or more, which means that as young fish begin to grow into the selection range they at first suffer only a low fishing mortality. As they grow larger, their chance of escaping from the net (having entered it) gets less, until, eventually, they are too large to escape at all; only then are they exposed to the full fishing mortality rate - whatever that may be. Although it is possible to introduce this progressive change of fishing mortality coefficient over the selection range into yield assessments, it is usually sufficient to represent the selection process by a single mean selection length l_c, and assume that all fish of length less than l_c are released, and that all those greater than l_c are retained by the gear, and experience the full fishing mortality.

The important quantity is therefore

t_c = mean selection age
= mean age of entry to the catch, or mean age at first capture.

In Figure 1 the mean selection length l_c is the length which makes the two shaded areas A and A' equal. If the selection curve is symmetrical, or nearly so, this will be the length at the mid-point of the curve, i.e. the 50% length, at which half the fish entering the net escape and half are retained. If the curve is not symmetrical, l_c can be calculated by equating areas between the selection curve, the line $l = l_c$, and the y-axis. Suppose the length scale is divided into small intervals, l_0, l_1 .... etc. of say 1 cm, and the corresponding ordinates are y_0, y_1 .... then the area to the left of the part of the selection curve between l_i and l_{i+1}, will be approximately equal to the rectangle $y_{i+1} - y_i$ high and $\frac{1}{2}(l_i + l_{i+1})$ long. The total area to the left of the curve is therefore $\Sigma \frac{1}{2}(l_i + l_{i+1})(y_{i+1} - y_i)$, which as the total height of the curve is 1, will equal l_c.

Recruitment is, by its nature, much less easy to express in quantitative terms than mesh selection. As the main interest is in the combined effect of recruitment and selection - i.e. the pattern of entry into the catch - the recruitment pattern is very important when it is above, or overlaps, the range of gear selection, but not when it is complete before gear selection starts. If therefore all fish have been recruited at a size below the selection range of any likely mesh size, then the precise pattern of recruitment may be ignored, and it can be taken arbitrarily as occurring at some convenient length or age below the selection range (cf. Fig. 1). Where

important, the general form of the recruitment curve may be determined by a proper knowledge of the biology of the species, and possibly estimated with greater accuracy by surveys, with research vessels, of the young fish both on and off the main fishing grounds. Failing this an estimate may be obtained by comparing the size composition of actual catches of commercial vessels with the known selectivity of the gear in use. Normally the recruitment will occur over a range of sizes, and may be described by the same type of curve as the selection curve of Fig. 1.

If selection and recruitment are occurring over the same range, as in Fig. 2a, then the effective selection, i.e. the proportion P_1 of the fish of a given size in the stock which are exposed to the full fishing mortality will be given by the equation

$$P_1 = r_1 \times S_1 \qquad \text{.....} \quad (6.1)$$

where r_1 = proportion recruited, i.e. ordinate of recruitment curve,

S_1 = proportion of those entering the net which are retained, i.e. the ordinate of the selection curve.

Thus the resultant selection curve, which expresses the effective entry of fish to the catch, is obtained as the product of the recruitment and mesh selection curves, and from it the resultant mean selection length can be determined as before by equating the two areas A, A'.

Sometimes, as in cases where the recruits migrate into a fishing area, recruitment, in terms of length, can be quite sharp, approaching in the extreme case knife-edge selection at a threshold length l_r, as in Fig. 2b. Fish below length l_r suffer no fishing mortality at all, since they are not within geographic range of the gear. But on reaching length l_r they are at once exposed to more than half of the full fishing mortality (as drawn in Fig. 2b). The resultant selection curve in this case therefore starts at length l_r and rises vertically to the selection curve of the gear; thereafter it is identical with the selection curve itself. Again, however, the mean selection length l_c can be calculated from this resultant curve by means of equation (6.1); in this case l_c is such that the two areas A and A' of Fig. 2b are equal.

6.2 Size limits

If a minimum legal size limit, l_s say, is set within or above the selection range of the gear in use, the entry to the landed catch can be represented by a curve which starts at l_s, and rises vertically until the true selection curve is reached (see Fig. 3). The mean selection length l_c is calculated by equation (6.1) and is such as to equalize the areas A and A' of Fig. 3.

Undersized fish will also be taken, and since they cannot be landed they must be rejected at sea. The effect of this capture and rejection on the yield from the stock depends on how many of the rejected fish survive. If all survive, the situation is the same as if the recruitment curve to the landed catch were the true selection curve.

If on the other hand, some or all undersized fish die after rejection, each year-class is subjected to a certain fishing mortality before it reaches length l_s, as represented by the lower part of the selection curve in Fig. 3 and by the mortality rate due to being caught and rejected. The resultant fishing mortality coefficient which takes account of the capture and rejection of undersized fish is obtained by calculating the mean of that part of the selection curve below the size limit by means of equation (6.1). Calling this mean length l_p, then it is such as to equalize the areas B and B' of Fig. 3. In other words, it is assumed that fish are not caught at all until they reach length l_p, and are then subjected to the fraction a of the full fishing mortality rate until they reach size l_s (a is the ordinate at length l_s, see Fig. 3). If growth from length l_p to length l_s occupies a period $t_s - t_p$ (see below) and the fraction q of rejected fish die, then the year-class is reduced by the factor

$$e^{-qa\,F\,(t_s - t_p)} \qquad \text{.....} \quad (6.2)$$

as a result of capture and rejection of undersized fish before it enters the marketable size range. In this expression F is the full fishing mortality coefficient to which fish are exposed when they have grown beyond the selection range of the gear.

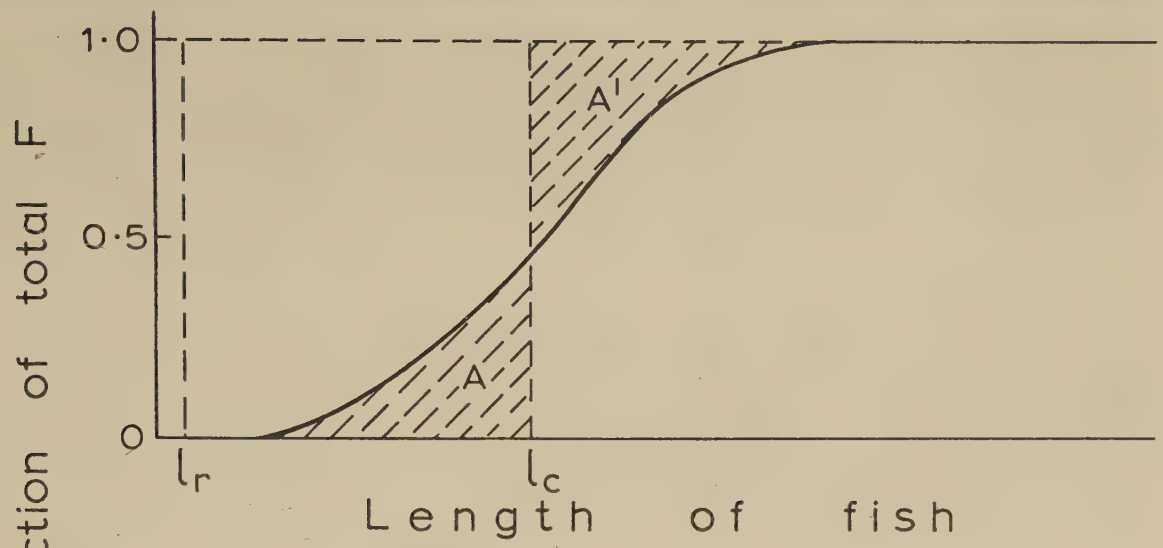


Figure 1. Simple selection curve

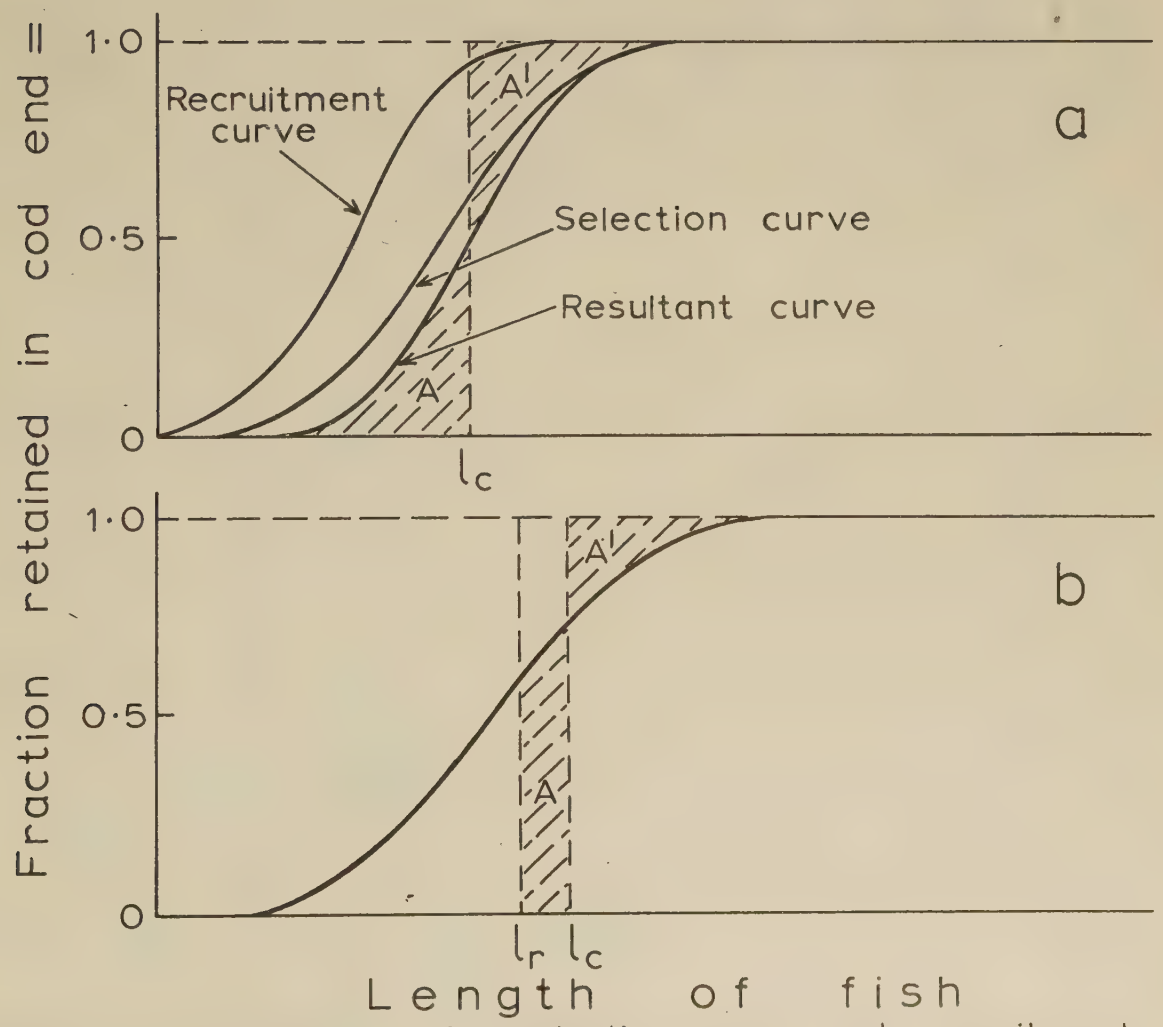


Figure 2. Combination of a selection curve and recruitment (a) recruitment over a spread of lengths (b) knife-edge recruitment.

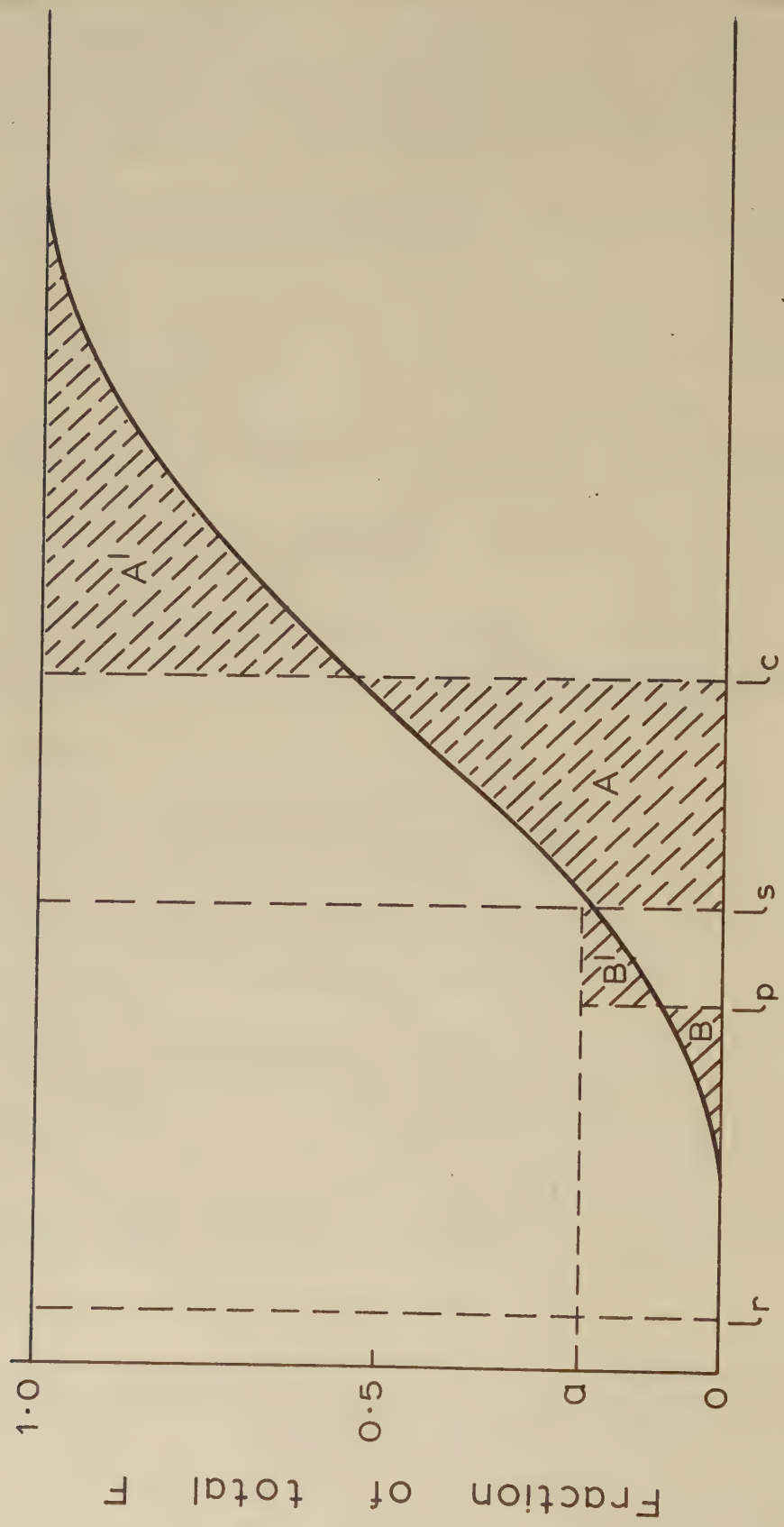


Figure 3. Effect of size limit (l_p) on the effective selection curve

6.3 Gill-net selection

The selectivity of gill nets is such that the proportion of fish retained is a maximum at same optimum size, and falls off for fish bigger or smaller than this optimum. If the size distribution of the fish in the fishing area can be determined directly by using some gear which is nearly unselective, or where selectivity is known, e.g. a trawl, then the selectivity of the gill net may be determined at once. That is, if the numbers of a given size, 1, of fish caught per unit fishing time are ${}_GN_1$, ${}_TN_1$, the fishing mortality exerted by the gill net on fish of length 1 will be proportioned to ${}^{G}N_1/{}_TN_1$.

When a non-selective gear cannot easily be used, then the selective properties are best estimated by using a range of gill nets of several different sizes. For any particular size of fish the distribution of catches by different mesh sizes will be analogous to the distribution of catches by a particular mesh size of different sizes of fish, having a maximum at some optimum mesh size, and falling off at each side. From the data of catches by different nets (adjusted if necessary to allow for different total fishing time by different mesh sizes) such distributions can be obtained for each size of fish. These can be continued by expressing both variables in standard terms - mesh size as the ratio of its perimeter to the girth of the given size of fish, or as a ratio of its size to the most efficient mesh size for that size of fish, and numbers of fish caught as a ratio of the numbers caught with the mesh used and with the most efficient mesh (cf McCombie and Fry, 1960, Gulland 1961b).

If it is assumed that each mesh has the same optimum fishing power, i.e. causes the same fishing mortality on the size of fish for which it is most efficient, then the combined data can be used at once to give not only the relative efficiences of different nets on a given size of fish, but for a net of a given mesh size, the relative efficiencies for different sizes of fish, i.e. its selectivity.

The selectivity may also be estimated by comparing catches of only two mesh sizes, provided some assumption is made concerning the form of the selection curve. This is often close to normal, and if it is assumed in fact to be normal, then putting

C_l = catch of fish of length l per unit fishing time

$$C_l = P_l \, P_m \exp\left(-\frac{(l-l_m)^2}{2S_m^2}\right)$$

where P_l = number of fish of length l liable to capture by the gear

P_m = fishing power of net of mesh size m

l_m = length of fish for which the mesh size m is most efficient

S_m = standard deviation of the mesh selection curve.

If two meshes, A and B are fished on the same population, then, in the obvious notation

$$ {}_AC_l/{}_BC_l = \frac{P_l \, P_A \exp\left(-\frac{(l-l_A)^2}{2S_A^2}\right)}{P_l \, P_B \exp\left(-\frac{(l-l_B)^2}{2S_B^2}\right)} $$

or, taking logarithms to base e,

$$ \log {}_AC_l = \log {}_BC_l = \log {}^{P_A}/_{P_B} - \frac{(l-l_A)^2}{2S_A^2} + \frac{(l-l_B)^2}{2S_B^2} $$

and assuming $S_A = S_B = S$, this reduces to

$$\log {}^{A}C_l/{}_{B}C_l = \log {}^{P_A}/P_B - \frac{l_A^2 - l_B^2}{2S^2} + \frac{l_A - l_B}{S^2}\, l$$

The right hand side is linear in l, that is can be expressed as a+bl, where

$$a = \log {}^{P_A}/P_B - \frac{l_A^2 - l_B^2}{2S^2}$$

$$b = \frac{l_A - l_B}{S^2}$$

Thus if the log of ratio of the catches per unit time of nets of different size are plotted against length the result is a straight line, from which can be estimated

$$b = \frac{l_A - l_B}{S^2} = \text{slope}$$

$$a = \log {}^{P_A}/P_B - \frac{l_A^2 - l_B^2}{2S^2} = \text{intercept.}$$

From this l_A, l_B and S^2 cannot be estimated separately, and hence the selection curves determined, without some extra assumptions; however it is reasonable to assume (as in the previous section for a range of mesh sizes) that the fishing powers of the two nets are equal, and also that the optimum length is proportioned to mesh size (usually in practice equivalent to a fish whose girth is slightly greater than - say 1.1 times - the perimeter of the mesh).

i.e. $l_A = K\, M_A$

$l_B = K\, M_B$

Then slope $= b = K\, \frac{M_A - M_B}{S^2}$

intercept $= a = -K^2\, \frac{M^2_A - M^2_B}{2S^2}$

From which $K - \frac{2a}{b\,(M_A + M_B)}$

$$S^2 = \frac{2a\,(M_A - M_B)}{b^2\,(M_A + M_B)}$$

and hence the selection curves can be determined.

When the selection curve of the gill net has been determined, subsequent population analysis is simpler if the curve can be represented by a more simple form, analogous to the knife-edge approximation to the trawl selection. Two selection lengths are needed, l_c, the length at which the fish enter the selection range, and l_m, at which they grow out of it. That is, the fishing with a gill net with the selection curves of Figure 4 has the same effect as a constant mortality between lengths l_m and l_c, where the pairs of shaded areas A and A', and B and B' are equal.

6.4 Conversion of Length to Age

The expressions above give selection in terms of length of fish. Population analysis is much simpler in terms of age, so that conversion from length to age is necessary. Though growth is usually seasonal, the growth curve is usually fitted to the average annual figures.

If the seasonal pattern is very marked, and all fish of a particular age are nearly the same length, the age at which a fish reaches a given length may depend critically on whether this length is reached near the beginning or the end of the period of rapid growth. If this is the case, the conversion of length to age is best made empirically from the observed age-length curve. Usually, however, it is sufficient to convert length to age from a growth equation fitted to all the observed data of length to age, e.g. the von Bertalanffy equation

$$l_t = L_{oo}\left\{1 - e^{-K(t-t_o)}\right\}$$

To obtain t in terms of l we divide both sides by L_{oo}, and subtract from unity, giving

$$\frac{L_{oo} - l_t}{L_{oo}} = e^{-K(t-t_o)}$$

Taking natural logs of both sides gives

$$\log_e \frac{L_{oo} - l_t}{L_{oo}} = -K(t-t\ )$$

and therefore $t = \frac{1}{K}\log_e \frac{L_{oo}}{L_{oo}-l_t} + t_o$ ..... (6.3)

The span of age $t_2 - t_1$ between two lengths l_1, l_2 is therefore

$$t_2 - t_1 - \frac{1}{K}\log\frac{(L_{oo} - l_1)}{(L_{oo} - l_2)}$$ ..... (6.4)

6.5 Exercises

1. (a) Cod-ends of 44 mm and 112 mm fished alternatively gave catches of plaice for equal fishing times as set out in Table 1.

   (b) A cod-end of 74 mm fitted with a small-meshed cover gave catches of whiting distributed between the cod-end and cover as in Table 2.

   Draw the selection curves for plaice and whiting from these data and determining the mean selection lengths (l_c). Note that the number entering the net is for (a) (alternate hauls) equal to the catch in the small-meshed net, but for (b) is the sum of the fish retained in the cod-end, and those which went through the meshes, i.e. in the cover.

2. An approximate recruitment curve for the English North Sea plaice fishery is as follows:-

Length (cm)	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Fraction recruited	0.02	0.05	0.08	0.16	0.27	0.38	0.48	0.62	0.75	0.86	0.94	0.97	0.99	1.00	1.00

   Calculate the resultant selection curve with a mesh of 112 mm (using the result from Example 1) and hence the value of l_c.

   If instead of the above recruitment curve, recruitment was found to be effectively "knife-edge" at 26 cm, what would be the value of l_c with a 112 mm mesh?

3. Convert the above estimate of l_c for plaice and whiting to age (t_o) using the von Bertalanffy equation and parameter values as follows:-

   Plaice: $K = 0.095$, $L_{oo} = 68$ cm, $t_o = -0.8$ years

   Whiting: $K = 0.32$, $L = 45.5$ cm, $t_o = -0.4$ years

Table 1. Plaice

Length (cm)	44 mm mesh	112 mm mesh
10	0	0
11	1	0
12	2	0
13	6	0
14	16	0
15	18	0
16	26	0
17	64	3
18	121	4
19	182	10
20	247	13
21	292	16
22	344	37
23	367	60
24	355	132
25	276	190
26	225	177
27	147	136
28	90	97
29	57	54
30	26	33
31	24	26
32	18	13
33	10	9
34	12	7
35	5	6
36	10	5
37	6	2
38	3	4
39	2	2
40	2	3
41	0	1
42	0	2
43	0	2
44	0	1
45	0	1
46	0	1
47	0	0
48	0	0

Table 2. Whiting

Length (cm)	Cod-end (mm)	Cover
10	0	0
11	0	0
12	0	3
13	0	7
14	0	21
15	0	27
16	0	23
17	0	19
18	2	20
19	3	83
20	23	219
21	68	302
22	89	256
23	79	154
24	115	55
25	106	42
26	87	18
27	63	7
28	55	0
29	38	2
30	34	0
31	11	0
32	11	0
33	6	0
34	9	0
35	5	0
36	2	0
37	1	0
38	1	0
39	0	0

Exercise 4. The percentage length distributions of cod caught by gill-nets and purse-seines at Lofoten in 1952 were as follows (data from Rollefsen 1952)

Length (cm)	65-	70-	75-	80-	85-	90-	95-	100-	105-	110-	115-	120+
Purse-seine	2	4	8	13	20	28	35	34	25	15	8	5
Gill-nets	0	2	5	15	30	50	45	27	15	5	2	1

Assuming there is no selection by purse-seines, determine the form of the selection curve of the gill-nets. What size of fish is caught most efficiently by gill-nets?

Exercise 5. Nine sizes of gill-net were used for catching salmon in the Frazer River in 1947 and 1948. The numbers of fish of sizes caught by each mesh (adjusted for different fishing times) were as follows (data adapted from Peterson 1954).

Fork Length cms	Mesh Size (cms)								
	13.5	14.0	14.8	15.4	15.9	16.6	17.8	19.0	20.6
50-1	6	4							
52-3	52	11	1	1	-	-	-	-	-
54-5	102	91	16	4	4	2	-	2	2
56-7	295	232	131	61	17	13	3	1	2
58-9	309	318	362	243	95	26	4	2	1
60-1	118	173	326	342	199	100	10	8	1
62-3	79	87	191	239	202	201	39	10	6
64-5	27	48	111	143	133	185	72	16	3
66-7	14	17	44	51	52	122	74	27	3
68-9	8	6	14	23	25	59	65	51	1
70-1	7	3	8	14	15	16	34	22	2
72-3		3	1	2	5	4	6	10	1
74-5								1	

(a) (Graphical method) By plotting for each size-group separately the numbers caught against mesh size, estimate the numbers of each size of fish which would be caught by the most efficient mesh for that size of fish. Hence express the catch of any mesh as a percentage of the potential catch by the most efficient mesh, i.e. the selectivity of that mesh size for that size of fish.

Combine these selection curves for all meshes by expressing the length of fish as a proportion of the length of fish caught most effectively by the mesh in question. Hence obtain a single combined estimate of the selection curve of a gill-net on salmon.

(b) (Analytic method) Calculate the logarithm of the ratio of catches of fish of a given size taken by pairs of adjacent mesh sizes. Assuming the selection curve for each mesh is normal and of constant variance, and that the mean selection length of any mesh is proportional to the mesh size, calculate the selection curve for each mesh.

Section II. ASSESSMENTS

7. UNIT STOCK

Before population theory can be applied to a particular situation it is necessary to determine to what extent the fish population and the fishery based on it can be treated as a unit system. There is no simple objective definition of what constitutes a unit stock, or a unit fishery, and the definition may be made purely on practical grounds. A group of fish can be treated as a unit stock if the results of assessments and other population studies in which it is treated as a unit stock do not diverge significantly from the real situation. This means, on one hand, that happenings external to the unit stock, e.g. fishing in other areas, do not have a significant effect, and on the other hand, that there are no sub-groups within the "unit stock" with significantly different population characteristics.

One corollary of this definition is that, as the precicision of the population studies increases, the choice of unit stock may also have to change. A group of fish may have sufficiently uniform characteristics to be treated as a single stock when these characteristics are known only roughly, but may have to be treated as two or more unit stocks, perhaps with certain mixing rates, each with different characteristics, as these characteristics become measured with greater precision.

A unit stock, as used here, does not necessarily correspond to a biological, or genetic, unit. Thus, if two species in an area have the same growth pattern and mortality rates and are fished on the same grounds by the same gears, then, at least in the early stages of analysis when data are scarce, it may be permissible to treat them as a single unit stock. Conversely, male and female plaice in the North Sea differ so much in growth, and in fishing and natural mortality rates, that for detailed analysis they should be treated as different "stocks", i.e. yield curves, etc should be calculated for the male and female populations separately, and the results for the plaice population as a whole obtained by addition.

While most of this course is concerned with the simple situation of a unit stock, or unit fishery, it is worth enumerating here some of the situations which cannot be treated as a unit stock or unit fishery.

(i) Distinct fish stocks which intermingle for some part of the year, and <u>are then fished</u>. Even if the separation of fish between the stocks at the end of the mixing period is perfect, the fishing mortality of the two stocks has an element in common, and neither can be treated as a unit unless the mixed catch can be separated into the elements from each stock (? Bank and Downs herring in the North Sea, ? Southern Bight and German Bight plaice).

(ii) Distinct stocks, fished separately, but with a significant amount of interchange between them (e.g. Iceland and Greenland cod).

(iii) A species inhabiting a large area with no obvious dividing features, so that any two groups of fish in adjacent areas mix freely together, but the mixing is slow enough for the fish at opposite ends of the area to be effectively independent (? many coastal species, ? North Sea whiting).

A determination of what can be treated as a unit stock will be made from a wide range of information, e.g.

(a) Distribution of the species. This will give an upper limit to the extent of the unit stock, while the presence of more or less effective barriers, e.g. a deep water channel for a strictly demersal species, may suggest sub-divisions which could behave as unit stocks.

(b) Spawning areas. A single compact spawning area suggests that the population is a biological unit at least so far as reproduction is concerned. Two or more distinct spawning areas suggest distinct spawning groups, though these may well mix as in types (i) and (ii) above.

(c) Catch and effort data. Common features in records of catch and effort data for adjacent fisheries over a period may indicate that they are acting on the same stock, and are parts of the same unit fishery.

(d) Age-composition data. Comparisons of the relative strength of year-classes in different areas may indicate the extent to which the fish in different areas are recruiting from the same source. Mortality rates, especially when combined with effort data, can be compared as in (c).

(e) Tagging. This may not always give reliable results (incomplete returns from some areas, etc), but under favourable conditions it is a valuable technique, being especially valuable as giving a mixing rate (when mixing takes place) which can be expressed in quantitative terms.

(f) Morphological or physiological characteristics. Genetic differences are good evidence of groups of fish being independent stocks, but the converse is not true. Characters which may be environmentally determined (e.g. vertebral counts) are less satisfactory, since differences can exist between groups of fish which are mixing but not mixing completely.

8. THE SIMPLE YIELD CURVE

Previous sections have been concerned with methods of collecting the basic data, and analysing them so as to obtain estimates of the basic population parameters - growth, mortality, age of recruitment, etc. This and later sections will be concerned with using these estimates to explain and understand the past history of the fishery, and to predict its future; in particular to predict the effect of changes in the pattern of fishing due to any proposed conservation or regulatory measure.

The simplest calculations are for a stock in which the various parameters are constant. For such a stock the calculations are best made in terms of the yield of a single year-class of fish throughout its life, which will be, in the steady state, the same as the annual yield from all year-classes present in the fishery. The whole lifespan can be divided into relatively short periods; for each period the number of fish alive, the number caught, the number dying of natural (non-fishery) causes, and the number surviving to the beginning of the next period can be calculated, and the yield, in weight, can be calculated as the product of the numbers caught and their average weight. This process can be done purely arithmetically, but for accuracy the periods chosen should be short, and therefore numerous, and the calculations are bound to be laborious. It is much easier to express the yield in an algebraic form, which has the great advantage of showing explicitly the influence of the various parameters on the yield.

We will define the terms as follows:-

N_t = number of fish alive at time t
R = number of recruits, i.e. the number of fish alive at age t_r
R' = number of fish alive at the age t_c at which they are first retained by the gear in use
M = instantaneous natural mortality coefficient
F = instantaneous fishing mortality coefficient;

then for $t_r < t < t_c$

$$\frac{dN_t}{dt} = -MN_t$$

i.e. the numbers dying of natural causes per unit time is equal to the product of the natural mortality coefficient times the number of fish.

$\therefore\ N_t = Re^{-M(t - t_r)}$, because $N = R$ when $t = t_r$

and $R' = Re^{-M(t_c - t_r)}$

and for $t > t_c$, when both fishing and natural mortalities are operating

$$\frac{dN_t}{dt} = -(F + M)N_t$$

and $$N_t = R'e^{-(F + M)(t - t_c)} \qquad \text{.....(8.1)}$$

or $$N_t = Re^{-M(t_c - t_r) - (F + M)(t - t_c)}.$$

The numbers of fish caught in the time interval t, t + dt will be $F.N_t dt$, so that the total numbers caught, C, will be given by dividing up the total time between t_c (the age at first capture) and t_1 (the maximum age attained) into short intervals, and adding the contributions from each interval.

Mathematically this is expressed by the integral

$$C = \int_{t_c}^{t_1} FN_t dt.$$

$$\therefore \quad C = \int_{t_c}^{t_1} FR'e^{-(F + M)(t - t_c)} dt$$

or, integrating

$$C = R'.\frac{F}{F+M}\left[1 - e^{-(F+M)(t_1 - t_c)}\right] \qquad \text{..... (8.2)}$$

which, if t_1 is taken as infinite, reduces to

$$C = \frac{FR'}{F+M} \qquad \text{..... (8.2')}$$

Thus, as would be expected, fishing takes a share of the total numbers reaching the age of first capture equal to the ratio of fishing mortality to total mortality

In the same way the weight caught in the time interval t, t + dt, is given by

$$Y_t = FN_tW_tdt$$

where W_t is the average weight of a fish of age t.

The total weight caught will therefore be given by

$$Y = \int_{t_c}^{t_1} FN_tW_tdt \qquad \text{..... (8.3)}$$

For this to be easily integrated, the expression for the weight has to be in a suitable form; of the growth equations discussed earlier, that of von Bertalanffy is one of the most convenient. That is, we can write

$$W_t = W_\infty\left\{1 - e^{-K(t - t_o)}\right\}^3$$

$$= W_\infty\left\{1 - 3e^{-K(t - t_o)} + 3e^{-2K(t - t_o)} - e^{-3K(t - t_o)}\right\}$$

Or, writing the right hand side as a summation,

$$W_t = W_\infty\sum_{n=o}^{3} U_n e^{-nK(t - t_o)}$$

where $U_o = 1$, $U_1 = -3$, $U_2 = 3$, $U_3 = -1$.

Then $$Y = \int_{t_c}^{t_1} F.R'W_\infty e^{-(F+M)(t - t_c)}\sum_{o}^{3} U_n e^{-nK(t - t_o)}dt$$

or, rearranging the terms

$$Y = FR'W_\infty\sum_{o}^{3} U_n\int_{t_c}^{t_1} e^{-(F+M+nK)(t - t_o)} e^{-nK(t_c - t_o)}dt.$$

$$\therefore\ Y = FR'W_\infty\sum_{o}^{3}\frac{U_n}{F+M+nK} e^{-nK(t_c - t_o)}\left\{1-e^{-(F+M+nK)(t_1 - t_c)}\right\} \qquad \text{..... (8.4)}$$

Again this expression may be simplified by putting t_1 to infinity, and the yield is given by

$$Y = FR'W_\infty\sum_{o}^{3}\frac{U_n e^{-nK(t_c - t_o)}}{F+M+nK}$$

or, substituting for R'

$$Y = FRe^{-M(t_c - t_r)} W_\infty \sum_0^3 \frac{U_n e^{-nK(t_c - t_o)}}{F + M + nK} \qquad \text{..... (8.5)}$$

Besides the total yield, some other quantities are important. Thus the yield is F times the average total weight of fish in the exploited phase, P', and therefore

$$P' = R'W_\infty \sum_0^3 \frac{U_n e^{-nK(t_c - t_o)}}{F + M + nK} \qquad \text{..... (8.6)}$$

Similarly, the average number in the exploited phase is, from equation (8.3)

$$N' = \frac{R'}{F + M} = \frac{Re^{-M(t_c - t_r)}}{(F + M)}$$

The average weight of the individual fish in the exploited phase is therefore

$$\bar{W} = {}^{P'}/_{N'} = {}^{Y}/_{C} = W_\infty \sum_0^3 \frac{U_n(F + M)e^{-nK(t_c - t_o)}}{F + M + nK}$$

Because the recruitment is unknown and often variable, the yields etc are normally calculated as yield etc per recruit.

The steps in calculating the yield directly from equation (8.5) have been set out in the attached work-sheets. The first (A) shows a layout for calculating yield for a range of values of fishing mortality, (F), selectivity (t_c) being constant. The entries in the box at the top left will be completed from the knowledge of the various parameters in the stock, either using the best estimates available, or, if the knowledge is not so precise, a range of values for natural mortality etc; a separate sheet is used for each set of possible values. The entries in the top middle deal with the calculations which are the same for all values of F. Below are four pairs of columns (B) and (C) corresponding to the four terms in the summation of equation (8.5). (For convenience most of the entries, columns etc have been labelled with letters; when referred to in later column headings they are enclosed in brackets, to avoid confusion with the letters used for mortality coefficients etc. In the second row of each column is shown the formula which will normally be used in computing the entry in that column, the third row shows what the entry represents in terms of the various parameters).

The other work-sheets (B i) and (B ii) are used for calculating the yield for varying selectivities. The first is used to calculate t_c and related quantities from the selectivity, which will normally be defined by the size at first capture l_c. The yield for the range of selectivities and any particular fishing mortality can then be calculated as on sheet (B ii), which is nearly the same as work-sheet (A).

The computational work can be shortened, particularly when several stocks are being studied, by rearrangement of the terms in equation (8.5)

Putting $J = Y/RW_\infty$

$$J = Fe^{-M(t_c - t_r)} \int_{t_c}^{\infty} e^{-(F + M)(t - t_c)} \left\{ 1 - e^{-K(t - t_o)} \right\}^3 dt$$

and putting $y = e^{-K(t - t_o)}$

$$J = Fe^{-M(t_c - t_r)} \int_0^x e^{-(F + M)(t_o - t_c)} y^{\frac{F + M}{K}} (1 - y)^3 \frac{dy}{Ky}$$

$$= \frac{Fe}{K}^{-M(t_c - t_r)} e^{-(F + M)(t_o - t_c)} \int_0^x y^{\left(\frac{F + M}{K} - 1\right)} (1 - y)^3 dy$$

where $x = e^{-K(t_c - t_o)}$

The integral part is an incomplete Beta function so that

$$J = \frac{Fe^{-M(t_c - t_r)}}{K} e^{-(F + M)(t_o - t_c)} Bx\left(\frac{F + M}{K}, 4\right)$$

$$= \frac{Fe^{-M(t_r - t_o)}}{K} e^{-F(t_o - t_c)} Bx\left(\frac{Z}{K}, 4\right)$$

where $Z = F + M$

and putting $J_o = J e^{-M(t_r - t_o)}$, i.e. referring the yield to a hypothetical recruitment at age t_o,

$$J_o = \frac{F}{K} x^{-F/K} Bx\left(Z/K, 4\right) \qquad \text{..... (7)}$$

This gives the yield per recruit, or strictly a quantity proportional to the yield per recruit, as the product of two quantities, for one of which the incomplete Beta function tables are available (cf. Jones, 1957; Wilimovsky and Wicklund, 1963) and for the other (Fx^F/K) tables can be constructed (cf. Holt, 1957). Now

$$x = e^{-K(t_c - t_o)} = \frac{L_\infty - l_c}{L_\infty}$$

i.e. it is the proportion of the total growth (in length) which is made up after the fish enters the exploited phase. Despite the apparent complexity of the expression for the yield, it is actually determined by only a few quantities: how much of its total potential growth the fish has completed when it is recruited, and the relative magnitudes of the fishing mortality, the natural mortality, and the growth parameter K.

Other forms for the yield can be obtained by substituting different formulae for the weight in equation (8.3). In particular, over any moderately short period of time, say t_1 to t_2, growth in weight may be treated as exponential;

$$\text{i.e.} \quad w_t = w_1 e^{g_1(t - t_1)} \qquad t_1 < t < t_2$$

where w_1 is the weight at time t_1.

The growth coefficient g_1 will change according to the interval chosen, generally decreasing with increasing age. Substituting, the yield in weight during the period $t_1 - t_2$ is

$$Y = \int_{t_1}^{t_2} F N_t W_t \, dt$$

$$= \int_{t_1}^{t_2} F.R' e^{-(F + M)(t_c - t_1)} e^{-(F + M)(t - t_1)} e^{g_1(t - t_1)} w_1 \, dt$$

$$Y = FR' w_1 e^{-(F + M)(t_c - t_1)} \frac{1}{F + M - g_1} \left(1 - e^{-(F + M - g_1)(t_2 - t_1)}\right).$$

The total yield may then be obtained by summing over the whole lifespan, using a sufficient number of intervals. An advantage of expressing growth in this form is that the size (or age) at which the total mass of a year-class is at its maximum is the size at which g is equal to the natural mortality coefficient M (the "critical size" of Ricker). The greatest yield is then obtained by taking all the year-classes as soon as they reach this size.

8.1 Exercises

A Effects of change in fishing intensity

A(i) North Sea plaice (75 mm mesh)

Approximate parameter values for North Sea plaice, with a 75 mm mesh, are as follows:-

$$M = 0.1$$
$$L_\infty = 68.5 \text{ cm}$$
$$W_\infty = 2860 \text{ gm}$$
$$K = 0.095$$
$$t_o = -0.8 \text{ yrs}$$
$$t_r = 3.7 \text{ yrs}$$
$$t_c = 3.7 \text{ yrs}$$

(a) Using worksheet A, calculate and plot against fishing mortality coefficient (F), curves of exploited population weight per recruit (P'/R) (proportional to catch per unit effort).

Yield per recruit (Y/R). Express this in gms, and also as a percentage of the present yield (i.e. with F = 0.5).

Exploited population numbers per recruit (N'/R).

Catch in numbers per recruit (C/R).

Average weight of fish in catch ($\overline{W}$).

(NOTE: Take F = 0, 0.1, 0.2, 0.3, 0.5, 0.7, 1.0, 1.5)

(b) Repeat the above with M = 0.05 and 0.15
(c) The present estimate of F for North Sea plaice is about 0.5. What percentage change in fishing intensity from the present level is needed to obtain the greatest steady yield per recruit?

By what percentage does this yield differ from the present level?
What effect would this change in intensity have on the catch per unit effort and the mean weight of fish in the catch?
How do these answers depend on the magnitude of M?
A(ii) Repeat for 140 mm mesh, given that t_c for this mesh size is 5.5 years.

A(iii) North Sea Haddock (75 mm mesh)

Approximate parameter values for North Sea haddock with a 75 mm mesh are as follows:-

$$M = 0.2$$
$$L_\infty = 55 \text{ cm}$$
$$W_\infty = 1300 \text{ gm}$$
$$K = 0.25$$
$$t_o = -0.2 \text{ yrs}$$
$$t_r = 1.0 \text{ yrs}$$
$$t_c = 2.1 \text{ yrs}$$

(a) Carry through the example A(i) (a), (d) and (e) as detailed above. N.B. The present estimate of F for North Sea haddock is about 0.8.

(b) Repeat with M = 0.1 and 0.3.

A(iv) Repeat for 100 mm mesh, given that t_c = 3.3 years.

B. Effects of change in mesh size

B(i) North Sea plaice (F = 0.5)

(a) For mesh sizes above 120 mm, the mean selection length l_c can be calculated directly from the selection factor (b) = 2.2. Using Worksheets B(i) and B(ii), with F = 0.5, calculate and plot against mesh size curves of P'/R, Y/R, N'/R, C/R and $\bar{W}$. Take M = 0.1 and other parameter values as listed in A(i). Express the yield as a percentage of the present yield; i.e. with a mesh of 75 mm.
(NOTE: Take mesh sizes of 120, 160, 180, and 200 mm, and also plot the values for meshes of 75 mm and 140 mm previously calculated for F = 0.5).

(b) Repeat with M = 0.05 and 0.15.

(c) What mesh size is needed to give the greatest steady yield per recruit with this value of F? By what percentage does this yield differ from the present level? What would be the corresponding changes in catch per unit effort and average weight of fish in the catch? How do these answers depend on the magnitude of M?

B(ii)

(a) Work through examples (a) - (c) as in B(i) above, but using F = 0.2 throughout.

(b) Compare your results and conclusions with those for F = 0.5.

B(iii) <u>North Sea haddock (F = 0.8)</u>

(a) The relation between mean selection length l_c and mesh size in haddock can be calculated with a selection factor of 3.2. Using Worksheets B(i) and B(ii), with F = 0.8 throughout, calculate and plot against mesh size curves of P'/R, Y/R, N'/R, C/R and $\bar{W}$. Take M = 0.2 and other parameter values as listed in A(iii).
(NOTE: Take mesh sizes of 80, 90, 120, 140. Plot also values previously calculated for meshes of 75 and 100 mm with F = 0.8).

(b) Repeat with M = 0.1 and 0.3.

(c) What mesh size is needed to give the greatest steady yield per recruit with this value of F? By what percentage does this yield differ from the present level? What would be the corresponding changes in catch per unit effort and average weight of fish in the catch? How do these answers depend on the value of M?

B(iv)

(a) Work through examples (a) - (c) as in B(iii) above, but using F = 0.3 throughout.

(b) Compare your results and conclusions with those for F = 0.8 and also with those for the North Sea plaice.

WORK SHEET (A)

FISHING INTENSITY ASSESSMENTS

Known data	
Species	
Mesh size	
M =	
W_∞ =	(gm)
K =	
t_o =	(yr)
t_c =	(yr)
t_r =	(yr)

$t_c - t_r =$

$M(t_c - t_r) =$

$e^{-M(t_c - t_r)} = \quad = (M)$

$W_\infty \; e^{-M(t_c - t_r)} \quad = (N)$

$t_c - t_o =$

$K(t_c - t_o) =$

$e^{-K(t_c - t_o)} = \quad = (D)$

$(B_n) = (F + M + nK) \quad (C_n) = \dfrac{U_n e^{-nK(t_c - t_o)}}{F + M + nK}$

			(G_n)
n	$(D)^n$	U_n	$U_n(D)^n$
0	1	+1	+1
1		-3	-
2		+3	
3		-1	-

	n = 0		n = 1		n = 2		n = 3							
(A)	(B_0)	(C_0)	(B_1)	(C_1)	(B_2)	(C_2)	(B_3)	(C_3)	(P)	(Q)	(R)	(S)	(T)	(V)
F	(A)+M	$1/(B_0)$	(A)+M+K	$(G_1)/(B_1)$	(A)+M+2K	$(G_2)/(B_2)$	(A)+M+3K	$(G_3)/(B_3)$	$(C_0)+(C_1)+(C_2)+(C_3)$	(P)x(N)	(Q)x(A)	(C_0)x(M)	(S)x(A)	(Q)/(S)
				-				-		P'/R	Y/R	N'/R	C/R	$\bar{W}$
				-				-						
				-				-						
				-				-						
				-				-						
				-				-						
				-				-						
				-				-						
				-				-						
				-				-						
				-				-						

WORK SHEET (Bi)

MESH SIZE ASSESSMENTS (i)

Known Data	
Species	
F =	
M =	
W_∞ =	(gm)
L_∞ =	(cm)
K =	
t_o =	(yr)
t_r =	(yr)
b	

Note $(D_n) = e^{-nk(t_c - t_o)}$

$(M) = e^{-M(t_c - t_r)}$

$(N) = W_\infty e^{-M(t_c - t_r)}$

(A)	(B)	(C)	(D_1)	(D_2)	(D_3)	(G)	(H)	(J)	(K)	(L)	(M)	(N)
Mesh Size (cm)	(A) x b	$(B)/L_\infty$	1 - (C)	$(D_1)^2$	$(D_1)^3$	$-\log_e (D_1)$	$(G)/K$	(H) + t_o	(J) - t_r	(K) x M	e - (L)	(M) x W_∞
	l_c	l_c/L_∞				$K(t_c - t_o)$	$t_c - t_o$	t_c	$t_c - t_r$	$M(t_c - t_r)$		

WORK SHEET (Bii)

MESH SIZE ASSESSMENTS (ii)

Known Data	
Species	
F =	
M =	
W_∞ =	(gm)
K =	
t_o =	(yr)
t_r =	(yr)
b =	

Note $(E_n) = U_n e^{-nK(t_c - t_o)}$

$$(C_n) = \frac{U_n e^{-nK(t_c - t_o)}}{F + M + nK}$$

	(F_n)
n	F + M + nK
0	
1	
2	
3	

	n = 0		n = 1		n = 2		n = 3							
(A)	(E_0)	(C_0)	(E_1)	(C_1)	(E_2)	(C_2)	(E_3)	(C_3)	(P)	(Q)	(R)	(S)	(T)	(V)
Mesh Size (cm)	(D_0)	$(E_0)/(F_0)$	$-3(D_1)$	$(E_1)/(F_1)$	$3(D_2)$	$(E_2)/(F_2)$	(D_3)	$(E_3)/(F_3)$	$(C_0)+(C_1)+(C_2)+(C_3)$	(P)x(N)	(Q)xF	(C_0)x(M)	(S)xF	(Q)/(S)
	1			-				-		P'/R	Y/R	N'/R	C/R	$\bar{W}$
	1			-				-						
	1			-				-						
	1			-				-						
	1			-				-						
	1			-				-						
	1			-				-						
	1			-				-						
	1			-				-						
	1			-				-						

9 SPECIAL ASSESSMENTS

The simple yield equation described in the earlier section depends for its calculation on fairly complete knowledge of the various parameters (growth, mortality, etc), and with this information it is possible to estimate the steady yield for any combination of fishing mortality and age at first capture. However, even if, as very often happens, information is far from complete, it is possible to answer certain specific equations, e.g. would a moderate increase in size of first capture increase or decrease the steady yield?

9.1 Catch and Effort Statistics

If statistics are available for a number of periods in which the effort was kept at a steady level it would clearly be possible to derive a purely empirical relation between fishing effort and steady yield, or catch per unit effort. In most fisheries there are few, if any, long periods of constant fishing effort, and the catch and catch per unit effort in any one year will be related not only to the effort in that year, but to the effort in several preceding years. However, the abundance of a particular year-class which has been in the fishery for say four years (i.e. is of age $t_c + 4$), will be governed by a factor equal to $e^{-(F_0 + F_1 + F_2 + F_3)}$ where F_0, F_1, F_2, F_3 are the fishing mortalities in the previous four years; i.e. its abundance will be the same as if it had been in a fishery with a steady fishing mortality of $\frac{1}{4}(F_0 + F_1 + F_2 + F_3)$. The total catch per unit effort (c.p.e.) of all ages is then related to some weighted mean of the fishing effort in the previous years. If this mean is taken over a period equal to the mean duration of life in the exploited phase (e.g. if the age at recruitment is four years old, and the major part of the catch, in weight, is made up of fish between four and nine years old, the mean duration is about three years), then the relation between this mean effort, $\bar{f}$, and the c.p.e. will be close to that between effort and c.p.e. in the steady state. The agreement will in fact be almost exact, not only when the effort has not altered greatly, but also when there has been a steady trend in effort. For instance if effort has been increasing, then the older ages will be over-abundant, having had an average fishing effort on them less than $\bar{f}$, while the younger ages will be too scarce, having experienced an average effort greater than $\bar{f}$.

This relation is best expressed graphically by plotting c.p.e. against $\bar{f}$; the best fit is usually not a straight line, but a curve concave upwards (for instance the curves for plaice or cod at Iceland,(Gulland) 1960). From this curve, giving the steady state relation between c.p.e. and effort, the corresponding relation between catch and effort can be determined at once by multiplication.

This approach is very close to the constant parameter model of the complete yield curve, in which density dependent effects are ignored, as most of these take effect over longer periods of time. For instance, in the example above, if recruitment is affected, the present stock is the offspring of the stock on the average six to seven years earlier, which in turn was determined by the fishing over the previous three years or more.

The major advantage of this method is that it requires easily obtainable data; total catch is usually known, and effort or c.p.e. data are usually among the earliest semi-scientific data to be collected. If there are errors in the effort data (the most likely being uncorrected trends, such as increased efficiency), these will affect both x and y values in the plotting, and tend to displace the points along the line $y = a/x$. This line is similar to the general form of the expected regression, so that it appears that errors in effort measurement will not distort the estimate of the relation between c.p.e. and effort, but may make the statistical significance of the fit greater than it really is. If the series of data is long enough the effect of changes other than simply of total effort may be studied. Thus if there has been a change in fishing practice, e.g. an increase of mesh size, in the middle of the series, then, if this has had a significant effect on the stock, two different regressions of c.p.e. on effort for the periods before and after the change could be determined.

9.2 Schaefer's Model

Another method of analysis depending chiefly on catch and effort data is that of Schaefer (1954, 1957). The population size, P, is considered as a single entity, which would, if fishing were not present, increase at a rate determined by its size, i.e.

$$\frac{dP}{dt} = f(P)$$

where f(P) is some function of P, being zero when P = 0, and when P is at its maximum P_M, and f (P) will have a maximum at some intermediate value of P.

Therefore, when fishing is present $\frac{dP}{dt} = f(P) - Y = f(P) - FP$
where Y = catch.

Clearly the population will remain constant if $Y = f(P)$, so that at any population size there will be a certain equilibrium catch, and this will be a maximum when $f(P)$ is a maximum.

The form of $f(P)$ may be determined from data on catch and effort, provided there is also some information (e.g. on tagging) from which catch per unit effort figures can be converted into absolute terms, i.e. if the coefficient q (k_2 in Schaefer's notation) is known. Thus if the values of catch per unit effort are known at the beginning and end of a year

initial population $= P_1 = {}^1/_q\,({}^Y/_f)_1$

final population $= P_2 = {}^1/_q\,({}^Y/_f)_2$

mean population $= \bar{P} = \frac{1}{2}(P_1 + P_2)$

$f(\bar{P}) = P_2 - P_1 + Y$

where Y is the catch during the year.

A pair of values of $f(\bar{P})$ and $\bar{P}$ can therefore be obtained for each year, and by plotting one against the other the relation between equilibrium catch and stock size may be established. The fitting may be made more quickly if some form for $f(P)$ is assumed, e.g. the logistic

$$f(P) = a\,P\,(P_M - P),$$

which gives a parabola. This form of curve is best fitted by plotted ${}^{f(P)}/_P$ against P, which gives a straight line. This method of analysis has much in common with that of the previous section. Both attempt to obtain the equilibrium relation between catch and effort (or one of its transformations) by suitable adjustment of data from a changing fishery - one by taking into account effort data in earlier years, and the other, changes in the catch per unit effort.

9.3 Changes in Selectivity

Many of the effects of changes in selectivity can be determined purely from a knowledge of the size composition of the landings (see Gulland, 1961b, 1964). Thus, immediately following a change in gear there will be no change in the stock, and the numbers of any given size, l, of fish landed by the new gear (e.g. increased mesh size) will be given by:

$${}_lN_k = {}_lN_1\ {}_lr_2/{}_lr_1 \qquad \text{.....(9.1)}$$

where ${}_lN_1$ = numbers landed by old gear

${}_lN_k$ = numbers landed by new gear

${}_lr_1$ = proportion retained by old gear

${}_lr_2$ = proportion retained by new gear.

If also ${}_lW$ = average weight of fish of length l then the total weight W_1, caught with the old gear, is given by:

$$W_1 = \sum_l {}_lW_l N_1 \qquad \text{..... (9.2)}$$

and weight caught with the new gear, W_k, is:

$$W_k = \sum_l {}_lW_l N_k \qquad \text{..... (9.3)}$$

we will also define $N_1 = \sum_l N_1$, $N_k = \sum_l N_k$.

(If the average weights ${}_lW$ and the relevant numbers are arranged as parallel columns these calculations of sums of products are simple to carry out on most calculating machines). The actual immediate change in landings can be expressed as a proportion L of the initial landings, where

$$L = \frac{W_1 - W_k}{W_1}.$$

When an increase in mean selection length takes place the fish released by the new gear, but which could have been caught by the old gear, will grow, and after a time reach the size at which they will

be retained by the new gear, and the catches will increase.

The number, N_R, of fish released will be equal to $N_1 - N_k$, or, if quantities of small fish are caught and discarded at sea, and not landed, by

$$N_R = \sum_l {}_lN_c \left(1 - {}^{l}r_2/{}_lr_1\right) \qquad \text{..... (9.4)}$$

where ${}_lN_c$ are the numbers of fish of length l caught by the old gear. Of these fish a number $N^1_R = N_R\, e^{-Mt}$ will survive to ${}_2t_c$, the mean age of first capture with the new mesh, where t is the difference between ${}_2t_c$ and the average age of the fish released. In turn, of these fish a number $E\, N^1_R$ will ultimately be caught, where E is the exploitation rate (= $F/F+M$ when the mortalities are constant). As all the mortalities etc for fish greater than ${}_2l_c$ are unchanged, the size distribution of these fish will be the same as that of the N_k fish, so that after a period the catches with the new gear will be increased by a proportion Q, when

$$Q = \frac{E\, N^1_R}{N_k} \qquad \text{..... (9.5)}$$

Thus the long-term landings, W_2, will be given by

$$W_2 = W_1\ (1-L)(1+Q) \qquad \text{..... (9.6)}$$

This level of landings may not be reached for several years after the change in selectivity. The interim effects may be estimated from the fact that if it takes an average time t^1 for released fish to grow to a certain length l^1, then after a time t^1 fish smaller than l^1 will have received the benefit of the change, but not those larger than l^1, and the landings will be equal to W^1, where

$$W^1 = \sum_{o}^{l^1} (1+Q)\ {}_lw_lN_k + \sum_{l^1}^{\infty} {}_lw_lN_k$$

i.e.

$$W^1 = Q \sum_{o}^{l^1} {}_lw_lN_k + W_k \qquad \text{..... (9.7)}$$

The method can be extended to stocks fished with more than one gear, some of which may not change their selectivities. Here equations (9.1) and (9.3) are applied separately to each fleet to find the immediate effects. The factor Q will be the same for all, and is given from the extension of equation (9.5) in the form:

$$Q = \frac{E\Sigma N'_R}{\Sigma N_k} \qquad \text{..... (9.8)}$$

where the summation of N_k includes the fish caught by all gears (omitting any fish, caught by gears whose selectivity does not change, smaller than the new selection length), but the summation of N_r will, of course, only include gears whose selectivity changes. The calculations necessary to assess the results of a mesh-change when two gears, possibly catching different sizes of fish, are operating are set out in the work-sheet on p. 9:7.

9.4 Interacting Fisheries

The above methods may also be used to study the interaction of different fisheries, particularly of a fishery (A) principally for one species (e.g. herring) which incidentally catches young fish of another species (e.g. haddock), which, when older, is itself the principal object of some other fishery (B).

The steps are again:

1. Calculate the number of fish caught by fleet (A), or the extra number being caught compared with what would have been caught supposing fleet (A) was complying with some desired regulation (= N).

2. Calculate the reduced numbers of these which will survive until the age of first capture of fleet (B) (= N^1).

3. Compare the numbers of these = EN^1, which would be caught, with the present catch, C, of fleet (B). Then the increase in the catches of fleet (B) which would take place if fleet (A) stopped fishing, is, as a proportion of the present catch: EN^1/C. (The same result may be obtained by comparing N^1 with the numbers of fish recruiting to fleet (B), which is C/E). (see ICES, 1960).

9.5 Exercises

1. The table below gives the catch per unit effort (catch, in tons, per 1,000 ton-hours' fishing by English trawlers) and the total catch, in thousands of tons, of cod and haddock, at Iceland.

	Total Catch		Catch/Effort			Total Catch		Catch/Effort	
Year	Cod	Haddock	Cod	Haddock	Year	Cod	Haddock	Cod	Haddock
1906	105	35	0.97	0.55	1936	280	25	1.14	0.14
1907	115	30	1.03	0.49	1937	295	25	1.39	0.11
1908	125	31	1.20	0.54	1938	305	24	1.11	0.16
1909	115	28	1.05	0.57	1939	198	13		
1910	135	30	1.12	0.56	1940	148	20		
1911	155	31	1.26	0.58	1941	158	15		
1912	160	28	1.20	0.47	1942	176	17		
1913	180	26	1.27	0.38	1943	189	13		
					1944	220	12		
1919	130	35	1.41	1.01	1945	216	14		
1920	190	53	1.39	0.70	1946	237	28	1.84	0.63
1921	175	37	1.16	0.58	1947	246	33	1.46	0.42
1922	220	40	1.27	0.61	1948	293	52	1.27	0.32
1923	220	38	1.09	0.44	1949	315	66	1.17	0.37
1924	300	38	1.09	0.30	1950	321	60	0.98	0.24
1925	320	35	1.28	0.31	1951	327	54	0.94	0.19
1926	295	37	1.09	0.32	1952	392	45	0.91	0.18
1927	340	54	0.99	0.38	1953	515	53	1.11	0.18
1928	360	57	0.88	0.34	1954	546	62	1.01	0.17
1929	390	54	0.83	0.29	1955	537	64	1.04	0.21
1930	490	49	1.10	0.28	1956	482	62	1.02	0.19
1931	475	40	1.09	0.21	1957	453	76	0.81	0.16
1932	480	32	1.34	0.19	1958	511	70	0.80	0.14
1933	510	26	1.28	0.14	1959	454	64	0.68	0.18
1934	480	26	1.14	0.14	1960			0.64	0.18
1935	400	27	1.16	0.14					

(a) Calculate the total fishing effort, in English units, on cod and on haddock each year.

(b) If the average duration of life in the fishery is two years for haddock and three for cod, relate the stock abundance to the past fishing effort. Is there any suggestion that either of these relations has changed?; in particular, examine the haddock curve for the years since 1950, when a larger mesh was introduced and trawling was banned in certain areas, including some nursery areas.

2. The table below gives data on catches and catch per unit effort of blue whales in the Antarctic. Taking alternative values of the population size corresponding to a catch per unit effort of 1.00 as 20,000 and 30,000 whales, calculate the change in population size each year, and hence the sustainable yield each year. Plot this against population size in that year, and that five years earlier (assuming blue whales recruit to the exploited stock at five years old). How may the catch data for the years 1939-1946 be used?

What is the maximum sustainable yield, and at what population size is it taken?

Year	Total catch	Catch per unit effort
1925/26	4,697	3.30
1926/27	6,545	3.76
1927/28	8,334	4.39
1928/29	12,734	4.49
1929/30	17,898	3.13
1930/31	29,410	3.71
1931/32	6,488	4.83
1932/33	18,890	4.61
1933/34	17,349	4.76
1934/35	16,500	3.46
1935/36	17,731	3.96
1936/37	14,304	2.83
1937/38	14,923	2.00
1938/39	14.081	1.77
1939/40	11,480	
1940/41	4,943	
1941/42	59	
1942/43	125	
1943/44	339	
1944/45	1,042	
1945/46	3,606	1.36
1946/47	9,192	1.85
1947/48	6,908	1.12
1948/49	7,625	0.98
1949/50	6,182	0.80
1950/51	7,048	0.81
1951/52	5,130	0.63
1952/53	3,870	0.44
1953/54	2,697	0.42
1954/55	2,176	0.31
1955/56	1,614	0.37
1956/57	1,512	0.27
1957/58	1,690	0.28
1958/59	1,187	0.18
1959/60	1,228	0.14
1960/61	587*	0.105
1961/62	639*	0.093

* Omitting pygmy blue whales

3. Data for the English trawl fishery for haddock at Faroes are given below, showing the numbers landed in each 5 cm length group, their average weight, and the proportion of each group retained by a 90 mm and a 120 mm mesh.

Length (cm)	Average weight (gm)	Percentage retained 90 mm	120 mm	Numbers landed (thousands)
25-29	160	50	3	8
30-34	260	80	16	314
35-39	420	98	41	1,084
40-44	630	100	72	1,409
45-49	880	100	94	1,370
50-54	1,190	100	100	952
55-59	1,570	100	100	465
60-64	1,760	100	100	255
65-69	2,530	100	100	124
70-74	3,100	100	100	73
75-79	3,800	100	100	30
80+	4,600	100	100	9

(a) What is the present total weight landed?

(b) If the present mesh was 90 mm, what would be the reduction in catch (as a percentage) immediately following an increase to 120 mm?

(c) If it takes an average of six months for the fish released to grow to the size of first capture of the 120 mm mesh, what would be the long-term effect of an increase of mesh to 120 mm, assuming that there is no other fishery, and that the natural mortality of fish in the selection size is 0.2, and E (= $^{F}/_{F+M}$) = 0.5?

(d) What would be the long-term effects on both fleets (as percentages, and actual weights) if there was also a line fishery operating, taking an average annual catch of five million fish weighing 6,000 tons, and E = 0.7? Assume all line-caught fish are larger than the selection size of the 120 mm mesh.

(e) What would be the effects if the trawlers discarded 30% of the catch (by numbers), and these fish were all small enough to escape through a 120 mm mesh? (Let Δ t = one year, say).

4. The average annual catch of haddock by trawlers fishing for herring in 1954-1956 was as follows:-

Size	Weight caught (tons)	Weight landed (tons)	Fish (millions)
Under 24 cm	2,500	-	25
24-27 cm	6,000	-	45
Over 27 cm	23,500	14,000	80
Total	30,000	14,000	150

The fishery for haddock lands on an average 70,000 tons per year, of fish whose average weight is 330 gm.

If the herring trawlers were to use a mesh of the minimum size for demersal fishing, what would be the effect on the haddock catches?, assuming:

(a) the legal mesh releases all haddock less than 24 cm;

(b) in the haddock fishery some 100 million fish over 24 cm are caught, but are rejected as being below the marketable size of 27 cm;

(c) the fish below 24 cm which would be released by a larger mesh take an average of six months to grow to 24 cm, during which time they would suffer a natural mortality of 0.2;

(d) E = $^{F}/_{F+M}$ = 0.8 (where F includes all forms of fishing).

Work sheet for assessing changes in selectivity (for two gears with different size compositions of their catches

Part I. Immediate Effects

(A)	(B)	(C)	(D)	(E)	(F)	(G)	(H)	(F)	(G)	(H)
				(D)/(E)						
		Proportion Retained			(F)x(1-(E))		(F)x(E)	(F)x(1-(E))		(F)x(E)
					Numbers for Gear A			Numbers for Gear B		
l	l^W	l^r_1	l^r_2	l^r_2/l^r_1	l^N_1	l^N_R	l^N_K	l^N_1	l^N_R	l^N_K

$\sum l^N$	___	___	___	___	___	___
$\sum l^N x_l^W$	___	___	___	___	___	___

$L = \frac{W_R}{W_1}$ _____ _____

Part II. Long term Effects

N_R: Number Released

Gear A
Gear B
Discards: _____
Total: _____

N_K: Number in catches immediately after change

Gear A
Gear B
Non-regulatory gears: _____
Total: _____

N_R/N_K = _____

Δt =

$\frac{1}{2} M\Delta t$ =

$e^{-\frac{1}{2}M\Delta t}$ =

$N_R/N_K \, e^{-\frac{1}{2}M\Delta t}$ =

			Gear A		Gear B	
E	Q	1+Q	(1-L)(1+Q)	G	(1-L)(1+Q)	G

$Q = E \, N_R/N_K \, e^{-\frac{1}{2}M} \, t$

$G = 1 - (1-L)(1+Q)$

10. CHANGES IN THE PARAMETERS

In the previous section all the parameters (growth, mortality, etc) have been assumed to be constant, except for the explicit changes in the fishing mortality or the age at first capture. In fact changes in all are possible, and some, e.g. the annual recruitment, can vary very widely. These changes may be the result, directly or indirectly, of changes in the abundance of stock (and hence possibly influenced by fishing), or be independent of the stock, and the result of changes in the environment - amount of food, etc. The latter can be divided, according to the effect produced, into two types of change. First there are those that alter the shape of the yield curves, so that the results of e.g. an increase of mesh size may be quantitatively different, and secondly those that only affect the height of the yield curve, and which therefore for many purposes can be neglected.

The best example of the second is the big variation that can occur, independent of changes in adult, spawning, stock, in the strength of successive year-classes of many fish, e.g. in haddock, herring, etc. Calculations omitting data on year-class change may suggest that an increase of mesh size from the present (say 100 mm to 110 mm) may increase the steady yield by say 5%. From this it need not be true that, if the mesh were increased, the yield in some particular future year would be exactly 5% greater than the present, because the year-classes then being fished may be of different strength. What is true (if the calculations are correct) is that the yield would be 5% above what it would have been if the old, 100 mm, mesh had been in use. For many practical questions (e.g. is a change from 100 to 110 mm advisable?) the differences due to change in recruitment are not of significance. For this reason, and because, as may be seen in the previous section, that is the form in which the expression for the yield is often obtained, many assessments are stated in the form of yield per recruit. An exception is when the amount of fishing depends critically on the strength of the year-class in the fishery, there being little or no fishing when year-classes are weak. A good example is the haddock fishery on St. Pierre Bank, where there was a big fishery on the outstanding 1949 year-class between 1953 and 1957, with little before or since.

Growth changes can have an effect on the shape of the yield curve, particularly that relating yield to size at first capture. In a heavily fished stock the maximum yield may be obtained with a size at first capture, l_c, not far below the maximum size, L_∞, but if there is a change in growth with a new and smaller L_∞, not many fish may survive to l_c and the yield with that value of l_c may be small.

10.1 Density Dependent Effects

While some changes in the environment may mean that the shape of the yield curves in the future will be different from those under the present conditions, density dependent effects can mean that the real yield curve is different from that calculated on the assumption of constant parameters. If the stock increases, e.g. following a reduction in fishing, the likely effects are that natural mortality will increase, and the growth decrease, but that the recruitment will increase. These effects act in opposite directions, the first two reducing the yield at high stock levels (i.e. at low fishing intensities, or with a large mesh size), but the last increasing the yield under these conditions of fishing. In a heavily fished stock, where reduced fishing or increased mesh size would be expected to increase the yield, density dependent mortality and growth have a damping effect, tending to make the yield curve flat, but the recruitment effect will exaggerate the changes. Density dependent recruitment is therefore rather the more critical effect.

If a relation can be established between any particular parameter and stock abundance, then it is possible to incorporate this into the simple yield equation. Usually it is not possible to produce an explicit mathematical expression for the stock or yield when a parameter changes with stock density, but estimates of stock and yield may be obtained for any given conditions of fishing effort, etc by successive approximations. For instance, if natural mortality is proportional to stock abundance, then to calculate the yield and stock at say twice the present fishing, we can take a first estimate of a halved stock, and therefore halved M; using this value of M in the equations will give a better estimate of stock, hence of M, which in turn can be used to provide better estimates.

In fact it is often impossible to determine the density effects on the various parameters, especially of natural mortality, and it is probably best to take certain likely relations and see how these affect the shape of the yield curve (cf Beverton and Holt, 1957, Section 18).

In studying the effect on recruitment two quantities may be related to stock size - the recruitment, i.e. the absolute number of young fish produced from a given stock, and the survival, i.e. the numbers of young per million eggs. If, as is sometimes assumed, recruitment is constant, at least over the range of probable stock sizes, use of both relations may therefore show whether a non-significant (in the statistical sense) relation between stock and recruitment is caused by a real and significant (in the biological and practical sense) change in recruitment with stock size which is obscured by variation in the data, or whether the average recruitment is really constant. The second

alternative should be detectable by a relation between survival and recruitment.

10.2 Exercise

1. The spawning stock of North Sea plaice may be estimated as the catch by weight per 100 hours' fishing by English trawlers, and the recruitment as the catch in numbers per hours of four year old fish four years later. Available data for the past years are given below. (from Beverton, 1961).

Year	Stock (cwt)	Recruitment	Year	Stock (cwt)	Recruitment
1926	16	18	1943	120	18
1927	15	28	1944	140	16
1928	16	61	1945	150	33
1929	16	36	1946	76	32
1930	17	27	1947	54	45
1931	16	18	1948	44	22
1932	16	28	1949	35	20
			1950	33	23
			1951	31	9
			1952	32	22

Calculate an index of survival from eggs to recruitment.

What is the relation (a) between stock and recruitment; (b) between stock and survival.

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Documents in this group are provisional editions of volumes or sections of FAO MANUALS IN FISHERIES SCIENCE, usually in the language of the original draft. They are given a limited distribution for comment by collaborators in this project, and for use of FAO headquarters and field staff and at training centers, courses and seminars. Revised versions are subsequently published by FAO in the official languages of the Organization.

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FB/58/T3	Part I - Physical and Chemical Methods in Meteorology and Oceanography	January 1958
	Part II - Laboratory Methods on Plankton and Benthos	February 1958

Revised versions of these have been combined with the Field Methods Manual to produce a "Manual of Methods in Fisheries Biology," the definitive text of which will be published in three language versions as **FAO Man. Fish. Sci.,** (1) (in preparation). A provisional English edition of **FAO Man. Fish. Sci.,** (2) "Fisheries Science" was issued for FAO by CSIRO, Cronulla, Australia, in 1960.

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